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Context-Dependent Contributions to Cooperative Behaviours

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master of Science in the Faculty of Science

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School of Biological Sciences, September 2018

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Abstract

Cooperative behaviours are found throughout nature, with contributions highly variable between and within individuals. Contributions are affected by fixed and long-term variables such as gender, age and dominance status, as well as shorter term factors such as satiation, danger and audience, which form an individual's personal context. Sentinel behaviour (where an individual adopts a raised position to scan for danger and warn groupmates of the presence of predators) is a cooperative act which conveys benefits to group members, as well as providing benefits to the sentinels themselves. Here I manipulate satiation state, perceived danger level and the conspecific audience to investigate the relevance of context-dependency in sentinel contributions. In addition to standard measures of sentinel behaviour (time spent as a sentinel, number of bouts, bout duration), I use novel measures of within-bout investment to investigate sentinel contributions through proxies of attentiveness. Experiments show that dwarf mongoose (*Helogale parvula*) foragers were more likely to become a sentinel when satiated and when under increased danger level, whereas the presence of a neighbouring forager (audience) decreased contributions. Satiation level had the largest impact, with supplementary feeding causing investment in more and longer bouts, whilst changes in average head scanning rate provided evidence for an interaction between the effect of satiation and danger levels. These results demonstrate that sentinel contributions are strongly context-dependent, with effects seen in both overall and within-bout characteristics.

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Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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Table of Contents

Chapter 1: General Introduction

1.1 Cooperation

Cooperation, "a behaviour which provides a benefit to another individual" (West *et al*., 2007), is widespread in nature. Cooperative acts can be conceptualised using a simple payoff matrix, where an actor and a recipient can either incur a benefit or a cost from the behaviour of the actor (Figure 1.1a), with cooperative acts spanning both (+/+) and (-/+) actor/recipient payoffs. In all cases cooperation is seemingly contrary to one of the central tenets of Darwin's theory of evolution through natural selection — that individuals act selfishly — and is also exploitable in simple models by defection (Nowak, 2006). Yet cooperation is often integral to the evolution of complexity and organisation in living organisms.

a)

	+ to actor	**-** to actor
+ to recipient	Mutual Benefit	Altruism
- to recipient	Parasitism	Spite

b)

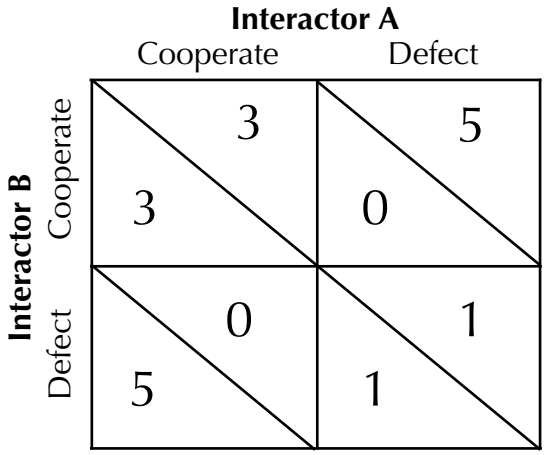


Figure 1.1 a) Payoff matrix of cooperative acts (adapted from West *et al*., 2007), with grey cells highlighting eventualities which can lead to cooperation. b) Payoff matrix from a classic Prisoner's Dilemma game (Adapted from Axelrod, 1987); such games were used first to conceptualise cooperation through reciprocity. The payoffs show that in one iteration of the game — one interaction — the best strategy is always to defect, regardless of what strategy the other player adopts.

One early explanation for the evolution of cooperative behaviours was 'kin selection', where individuals gain benefits through genes shared with relatives (Hamilton, 1964; Maynard Smith, 1964). Conceptualised using Hamilton's rule, and first elucidated by Haldane (1955), an individual will

benefit if the cost of the behaviour (c) is outweighed by the benefit (b) the recipient receives multiplied by the relatedness of the two individuals (r) — where r is between 0 and 1.

Hamilton's rule: cooperation is supported if $\mathbf{rb} \geq \mathbf{c}$

However, cooperation is often observed between non-relatives (Elfström, 1997; Krams *et al*., 2007; Clutton-Brock, 2009; Cheney *et al*., 2010), and even different species (often referred to as mutualisms; Holbrook and Schmitt, 2005; Bshary and Grutter, 2006; Bshary *et al*., 2006; Booksmythe *et al*., 2010), therefore kin selection cannot fully explain costly cooperative acts. In some cases, individuals can gain direct benefits from performing cooperative behaviours. Two groups of theories account for the majority of explanations: reciprocity and by-product mutualism. If interactions between two individuals are reduced to simple games where an individual can either cooperate or defect, such interactions can be conceptualised using the Prisoner's Dilemma (Figure 1.1b). This game-theoretical approach has driven explanations of cooperation between unrelated individuals through reciprocal acts, and produced strategies by which cooperation between unrelated animals can become stable (Axelrod and Hamilton, 1981; Nowak and Sigmund, 1993). From such game-theoretic origins, the theory of reciprocal altruism (Trivers, 1971) and multiple other reciprocity-driven theories have arisen (Nowak and Sigmund, 1993, 1998). For example, image scoring of individuals relating to their value can lead to indirect reciprocity (Nowak and Sigmund, 1998). On the other hand, by-product mutualisms describe cooperative acts between individuals that originally evolved through selfish behaviours of an actor, which incidentally conveyed benefit to a recipient. These evolutionary explanations are not necessarily mutually exclusive, with the potential for benefits to accrue pluralistically.

Cooperation is found throughout nature, with examples ranging from acts between conspecifics to those between members of different phyla. Cooperative interactions have been crucial in the evolution of complexity, and driven transitions between organisational levels (Leigh Jr and Rowell, 1995; Maynard Smith and Szathmary, 1997). At the organismal level, fungi and algae cooperate to

from lichens (Gargas *et al*., 1995), anemonefish cooperate with their host anemone (Holbrook and Schmitt, 2005), ants have evolved to tend to fungus gardens cooperatively (North *et al*., 1997), and groupers (*Plectropomus pessuliferus*) and giant moray eels (*Gymnothorax javanicus*) cooperate to increase prey capture efficiency (Bshary *et al*., 2006). Within species, individuals cooperate to achieve many goals. Cooperative provisioning of young through biparental care is seen widely, including in amphibians (Brown *et al*., 2010), fishes (DeWoody *et al*., 2000), mammals (Gubernick, 1994), birds (Cockburn, 2006), and invertebrates (Trumbo, 2012). Cooperating individuals often defend territories from other conspecifics: neighbouring rock pipits (*Anthus petrosus*) cooperate to evict intruders (Elfström, 1997), groups of subdesert mesites (*Monias benschi*) use cooperative displays to defend their home ranges (Seddon and Tobias, 2003), whilst cichlids (*Neolamprologus pulcher*) aggressively bite and chase away unfamiliar intruders (Frostman and Sherman, 2004). African wild dog (*Lycaon pictus*) packs cooperatively hunt to maximise prey capture (Creel and Creel, 1995), as do chimpanzees (*Pan troglodytes*) (Boesch, 1994). In many cases, a group size effect is seen: larger groups raise more young (Rood, 1980), increase foraging efficacy (Focardi *et al*., 2015) and provide more survival benefits than smaller groups (Bygott *et al*., 1979). Larger groups are also better able to defend larger, or higher quality, territories (Mosser and Packer, 2009); in these instances, the presence of many cooperators outweighs the costs of increased local competition.

In gregarious and group living species, behaviours have also evolved to help combat predation, which include alarm calling, predator mobbing and sentinel behaviour. Although there is some evidence that these behaviours are selfish (Clutton-Brock *et al*., 1999; Wheeler, 2008), they all convey survival benefits to other group members. Alarm calling, the production of specific sounds in the face of imminent danger, is widespread in mammals and birds (Caro, 2005; Hollén and Radford, 2009), with both conspecific and heterospecific receivers common (Caro, 2005; Magrath *et al*., 2015). In most instances alarm calls are given to potential predators, but in some cases have evolved to signal the presence of brood-parasites (Gill and Sealy, 2004). Alarm calls can be multi-functional, both signalling to the predator that they have been identified and warning others of the impending threat (Zuberbühler *et al*., 1999; Bergstrom and Lachmann, 2001). In some species, alarm calls have

evolved to provide threat-specific information: for instance, vervet monkeys (*Chlorocebus pygerythrus*), meerkats (*Suricata suricatta*) and fork-tailed drongos (*Dicrurus adsimilis*) all use different calls for different threat types (Seyfarth *et al*., 1980b; Manser, 2001; Ridley, 2007), whilst white-browed scrubwrens (*Sericornis frontalis*) alter their calling to indicate predator proximity (Leavesley and Magrath, 2005) and noisy miners (*Manorina melanocephala*) encode information relating to predator activity in their alarm calls (Cunningham and Magrath, 2017). Although some individuals may alarm call in isolation (Ostreiher and Heifetz, 2017), systems of functional reference would suggest the primary purpose of alarm calls in these cases is to provide better information to receivers.

Cooperative breeding, where non-breeding helpers aid in the raising of young that are not their own (Cockburn, 1998), has evolved in many taxa (Emlen, 1991; Jennions and Macdonald, 1994; Clutton-Brock, 2002; Koenig and Dickinson, 2004) and within these species cooperative acts are particularly prevalent. Group members cooperate to raise young (Rood, 1980; Taborsky, 1984; Dawson and Mannan, 1991), defend the territory (Radford, 2003; Jordan *et al*., 2007; Desjardins *et al*., 2008) and combat predation (Leavesley and Magrath, 2005; Graw and Manser, 2007; Bell *et al*., 2009). Helping behaviour may have evolved multiply through both kin-selection (Hamilton, 1964; Browning, 2012) and for direct benefits such as group augmentation (Kokko *et al*., 2001). In birds, for example, where helpers stand to gain territory by cooperating, direct benefits are the major predictor of interspecific variation in helper contributions (Kingma, 2017). A similar effect is found in cooperatively breeding fish: helpers are likely to contribute more if they are unrelated to the dominant breeding pair (Zöttl *et al*., 2013a). Where there is variation in relatedness in the brood, however, kin can be the driving force in helper contributions, with helpers preferentially provisioning young to which they are more related (Browning *et al*., 2012). Eusocial insects have taken such cooperation to extreme forms: in bees, wasps and ants, sterile worker castes have evolved to serve the queen and the wider colony (Wilson, 1978; Winston, 1991; Toth *et al*., 2007).

1.2 Variations in Contributions to Cooperative Behaviours

Considerable inherent variation exists between individuals of the same species, or even the same group, in their contributions to cooperative behaviour (Komdeur, 2006; Sanderson *et al*., 2015). However, many factors also generate within-individual variation on different timescales, from longer-term life-history traits such as gender, age, and dominance status, to more flexible, shorter-term fluctuations arising from changes in individual, environmental and social contexts.

1.2.1 Fixed and longer-term factors

Gender plays a major role in determining contributions in many species (reviewed in Sen, 1987), and how those contributions are modulated by other factors. A classic example is that of bi-parental care in raptors, where the female invests predominantly in the brooding of the clutch (Ketterson and Nolan, 1994), whilst the male catches prey to provision the young (Eldegard, 2003). In the extreme case of eusocial insects, only females participate in cooperative behaviours, with the male reproductive caste specialised to leave the nest and find a future queen with which to mate (Oster and Wilson, 1979). Whilst such gender roles are quite fixed, differential contributions can be more subtle. In meerkats, for example, weight gain is a predictor of sentinel contributions in males and pup-feeding in females, but not vice versa (Clutton-Brock, 2002), whilst males contribute more than females in the mobbing of venomous snakes (Graw and Manser, 2007). Similarly, female helper acorn woodpeckers (*Melanerpes formicivorus*) provide more food for the brood than male helpers (Koenig *et al*., 1983).

Dominance status, a characteristic the can change but tends to be fixed in the medium to long term, also influences cooperative contributions. For example, in Harris' hawks (*Parabuteo unicinctus*), beta and gamma males have only a small role in the care of eggs and young relative to the alpha, although they invest more equally in prey capture and defence against heterospecifics (Dawson and Mannan, 1991). Cichlid fish dominants participate more in territorial defence than subordinates (Desjardins *et al*., 2008), whereas green woodhoopoe (*Phoeniculus purpureus*) subordinates contribute more in territorial vocal rallies than dominants (Radford, 2003). Such differences are also seen in mammals:

subordinate meerkats perform almost all babysitting duties (Clutton-Brock *et al*., 1998), and whilst subordinate African wild dogs are the primary regurgitaters of food for pups in large packs, dominants perform more regurgitation than subordinates in small packs (Forssman *et al*., 2018).

Age is a characteristic that gradually changes for all individuals, and affects contributions to many cooperative behaviours through its correlations with size, experience and condition. For instance, larger, older cichlids contribute more in nest-digging behaviour, with the smaller, younger helpers contributing more in egg defence (Bruintjes and Taborsky, 2011); larger helpers in this species also contribute more than smaller helpers in territorial defence, especially when population density is higher (Bruintjes and Taborsky, 2008). Similarly, Damaraland mole rats (*Fukomys damarensis*) increase their cooperative contributions to tasks such as digging, nest building and food carrying with increasing age (Zöttl *et al*., 2016), whilst in larger groups of the cooperatively breeding white-winged chough (*Corcorax melanorhamphos*), contributions to incubation of the brood increase with age (Heinsohn and Cockburn, 1994). A more extreme example is that of age polyethism, where an individual changes its behavioural role with age, which is found throughout the eusocial insects (Oster and Wilson, 1979). For instance, honeybees (*Apis mellifera*) change from nurses to foragers as they become older (Seeley, 1982).

1.2.2 Context-dependent variation

1.2.2.1 Social context: contributions and audience

One well documented predictor of variations in individual contributions is the contribution of others. Heavily studied in models of parental care (Wright and Cuthill, 1990; Duckworth, 1992; Markman *et al*., 1995; Hinde, 2005; Zöttl *et al*., 2013b), individuals have been shown to increase their own provisioning effort when other individuals decrease theirs. Starlings (*Sturnus vulgaris*) and orange-tufted sunbirds (*Cinnyris bouvieri*) both increased their contributions to brood provisioning when their partner was impaired with tail weights (Wright and Cuthill, 1990; Markman *et al*., 1995), and female cichlid breeders increase their contributions when subordinate helpers are removed (Zöttl *et al*., 2013b). There is also experimental evidence with respect to subordinate alloparental care: Arabian

babbler (*Turdoides squamiceps*) helpers reduce their investment in line with an increase from other group members (Wright and Dingemanse, 1999), and the laziest carrion crow (*Corvus corone*) helpers increase their investment when the highest contributing helper is impaired (Baglione *et al*., 2010). Interestingly, in the examples of parental investment, compensation is incomplete — the increase from the unburdened partner is less than the decrease from the burdened partner(s) — yet in examples of alloparental investment, compensation is complete. This is likely due to the differing motives and goals of the classes of individuals in question; parents in pairs will likely incompletely compensate as to ward against a partner defecting, whereas subordinate helpers are more likely to gain other benefits from helping. There is also likely to be a threshold of maximum provisioning, which in larger groups will prevent all individuals maximising their provisioning effort.

Aside from models of parental care, contingent contributions are seen in a wide range of behaviours. Common vampire bats (*Desmodus rotundus*) will invest in cooperative blood sharing, but predominantly with individuals who have shared blood with them in the past (Carter and Wilkinson, 2013). Similarly, pied flycatchers (*Ficedula hypoleuca*) will only assist in the mobbing of predators with cooperating neighbours, but not those that defected from previous mobbing events (Krams *et al*., 2007). Contingency can also operate across behaviours: unrelated baboons (*Papio hamadryas ursinus*) are more likely to recruit to the mobbing calls of individuals with whom they recently groomed (Cheney *et al*., 2010), and vervet monkeys (*Chlorocebus pygerythrus*) are more likely to invest in coalitionary support if their recent grooming partner enters a conflict (Borgeaud and Bshary, 2015).

Another significant contributor to variation in cooperative contributions is the audience when an individual is making a decision. Defined as individuals that affect the behaviour of the actor (adapted from Matos and Schlupp, 2005), an audience can influence cooperative investment in multiple behaviours. For instance, long-tailed tits (*Aegithalos caudatus*) alter their investment into feeding nestlings depending on their social environment, with provisioning dependent on the demographic of other helpers at the nest (Adams *et al*., 2015), whilst false feeding — deception of group-mates by imitating brood-provisioning — by white-winged chough helpers does not occur when other helpers

are present to witness it (Boland *et al*., 1997b). Alarm calling is heavily influenced by the audience of the caller, with both the likelihood of calling, and the subsequent call type modulated. Carolina chickadees (*Poecile carolinensis*) are more likely to alarm call, and do so sooner, when in flocks of familiar individuals as opposed to strangers (Coppinger *et al*., 2018), whilst both chickens (*Gallus gallus*) and red-legged partridges (*Alectoris rufa*) give more alarm calls in the presence of a conspecific audience than when alone (Karakashian *et al*., 1988; Zaccaroni *et al*., 2013). In the latter case, an individual was most likely to call in the presence of its partner than other non-partner conspecifics (Zaccaroni *et al*., 2013). In addition to conspecific effects, heterospecific audiences have been shown to influence alarm calling, with fork-tailed drongos only giving alarm calls to terrestrial predators in the presence of foraging pied babblers (*Turdoides bicolor*) (Ridley *et al*., 2007). These increases in alarm calling in the presence of others, and the lack of calling when alone, not only evidences the effect of the audience on the alarm caller, but by extension the cooperative nature of such behaviour.

1.2.2.2 Individual context: satiation and danger

An increase in food availability, and therefore satiation, often increases cooperative contributions. In meerkats, helpers who show high provisioning effort in one breeding season often show reduced effort in the next, but this reduction of investment is eradicated if the helper is provided with supplementary food (Russell *et al*., 2003). In females of this species, weight gain is also predictor of pup-feeding rates (Clutton-Brock *et al.,* 2002). Similarly, when provided with supplementary food, helper moorhens (*Gallinula chloropus*) and Arabian babblers increase their provisioning rates (Eden, 1987; Wright and Dingemanse, 1999), as do both breeders and helpers of white-winged choughs (Boland *et al*., 1997a).

A decrease in deceptive contributions is also seen when supplementary food is provided, although distinctions between satiation and condition should be made. False feeding in white-winged coughs is almost completely eradicated when helpers are given extra food (Boland *et al*. 1997b). Similar conclusions were drawn from a study on carrion crowns, with helpers reducing the rate of false feeding when provisioned with extra food year round (Canestrari *et al*., 2010). In this study, breeding

individuals did not reduce their false feeding rate when they themselves were provisioned, highlighting the different pressures and trade-offs faced by different classes of individual within a single population. In many cases, however, more care needs to be taken to disentangle the effects of short-term satiation from those of longer term improvements in condition — both potential consequences of supplementary feeding. Increased personal condition is not to be conflated with satiation level (hunger level), as individuals of poor condition can be satiated whilst individuals in good condition can be hungry, despite their effects seemingly causing similar trends in behaviours. This conflation could explain the increased provisioning in meerkats, as weight gain correlates with supplementary feeding (Russel *et al*., 2003).

The level of danger perceived by an individual also influences its cooperative contributions. This is best seen in anti-predator behaviours such as predator mobbing and alarm calling. Individuals alter their response to mobbing calls based on the level of danger associated with recruiting. Red-breasted nuthatches (*Sitta canadensis*) produce stronger cooperative mobbing responses to alarm calls of black-capped chickadees (*Poecile atricapillus*) when the information encoded in the call suggests that the predator is small — a more relevant threat to the nuthatch — rather than large (Templeton and Greene, 2007). Pied flycatchers mob threats at nearby nests regardless of the contributions of others, but only mob threats at nests further away if that neighbour has previously cooperated (Krama *et al*., 2012), suggesting that they are modulating their cooperative responses relative to their own personal danger level. The same phenomenon is seen in other behaviour: for example, herring gulls (*Larus argentatus*) alter their alarm call structure and rate with increasing perceived threat (Shah *et al*., 2015). Whilst a change in call intensity or rate could be interpreted as subtlety in predator—prey communication, the altering of call elements is most likely functioning to warn and recruit other conspecifics.

1.2.3 Stimuli interaction

Despite the knowledge that stimuli often interact, studies rarely investigate the effects of interactions between short-term contexts on cooperative contributions. Whilst most studies focus on the effects of

one type of stimulus, especially when concerning investment into cooperative behaviours (Boland *et al*., 1997b; Wright *et al*., 2001c; Zaccaroni *et al*., 2013), it is widely known that animals integrate many stimuli simultaneously, and these stimuli often interact (Hebets and Papaj, 2005): cats (*Felis catus*) trained using orientation tasks showed multiplicative enhancement in their learning when both visual and auditory stimuli were provided (Stein *et al*., 1989), whilst adaptive responses to predator faecal presentations are suppressed in dwarf mongooses (*Helogale parvula*) by traffic noise playback (Morris-Drake *et al*., 2016). It was demonstrated that pied flycatchers integrated both personal danger level and previous neighbour contributions into mobbing decisions, with each context operating non-independently (Krama *et al*., 2012). However, in the majority of studies on the effects of context on cooperative behaviours and contributions, interactions have primarily been presented with regards to fixed and long term factors such as gender, age, dominance status and group size (Clutton-Brock *et* al., 1999; Canestrari *et al*., 2010; Kern and Radford, 2013). As it is known that short term contextual contributors can interact to influence other behaviours, it is possible that cooperative investments will be similarly affected.

1.3 Sentinel Behaviour

1.3.1 An overview

One specific example of cooperation in social groups is sentinel behaviour, for which various hypotheses have been proposed. Acting as a sentinel, where an individual adopts a raised or prominent position to watch for danger (Bednekoff, 2015), is a form of anti-predator behaviour that has evolved in several mammalian (Rasa, 1986; Clutton-Brock *et al*., 1999), and avian (Gaston, 1977; McGowan and Woolfendon, 1989; Wright *et al*., 2001b; Bell *et al*., 2009) species, as well as potentially in some fishes (Fox and Donelson, 2014; Brandl and Bellwood, 2015). The earliest suggested hypotheses for sentinel behaviour were rooted in kin selection (McGowan and Woolfendon, 1989); individuals will keep watch over their relatives at personal cost but will gain indirect fitness benefits (Hamilton, 1964; Santema and Clutton-Brock, 2013). Other theories have discussed whether sentinel behaviour is performed in a competitive capacity as a form of sexual signal or prestige (Zahavi, 1990; Zahavi and Zahavi, 1997), or whether it could evolve independently

through reciprocal altruism (Trivers, 1971). There have recently been the suggestions that sentinels may be exhibiting selfish behaviour driven by internal factors (Clutton-Brock *et al.*, 1999; Wright *et al.*, 2001a, 2001c), with the benefit to the rest of the group somewhat incidental — a byproduct mutualism (Clutton-Brock, 2002).

A key characteristic of sentinel behaviour is its coordination, which brings anti-predator benefits. Where sentinel behaviour occurs, it is less likely for there to be multiple sentinels or none than would be expected by chance. For example, in the Florida scrub jay (*Aphelocoma coerulescens*), the likelihood of an individual commencing a sentinel bout in the same minute a group member ended their bout was greater than expected by chance (McGowan and Woolfenden, 1989). This contrasts non-coordinated herd and flock species whose personal vigilance decisions are rarely affected by the vigilance of their group mates (Lima, 1995). A coordinated sentinel system has proven to be effective at reducing predation rates. For instance, meerkat sentinels produce more alarm calls than their foraging counterparts (Manser, 1999), Florida scrub jay sentinels are the most likely individuals to produce the first alarm call (McGowan and Woolfenden, 1989), and it has been calculated that pied babbler sentinels detect 97% of the attacks that foragers would not (Bednekoff, 2015).

Sentinels produce a range of vocalisations during their bout in order to communicate with their group mates as well as potential predators. The most common of these calls are alarm calls, vocalisations given in the event of immediate danger (Hollén and Radford, 2009). These calls benefit foragers by alerting them to the presence of a predator, and may benefit the alarm caller directly through perception or condition advertisement (Caro, 2005). In some cases, evidence for coordination via concluding vocalisations has been presented; Florida scrub jays produce soft calls before terminating their bouts (Barbour, 1977, cited by McGowan and Woolfenden, 1989), but these are yet to be proven as essential in the coordination of such vigilance. In many species, sentinels produce surveillance calls throughout their bout in order to alert the group of their presence (Rasa, 1986; Manser, 1999; Bell *et al.*, 2010). Often referred to as the Watchman's song, an analogy to medieval guards who would call out throughout the night (Wickler, 1985), these calls represent communication

between the sentinel and the rest of the foragers, with sentinels varying their surveillance calls to encode information about their environment (Bell *et* al., 2009; Kern and Radford, 2013). In addition to anti-predator benefits, the Watchman's song enables individuals to optimise their foraging/vigilance trade-off; pied babbler foragers display decreased vigilance and increased food intake in response to playback of sentinel surveillance calls (Hollén *et al*., 2008).

Intrapopulation variation in sentinel behaviour is found in relation to both individual and group characteristics. For instance, dominant female meerkats perform less sentinel activity than all other classes (Clutton-Brock *et al*., 1999). Male Arabian babblers perform more sentinel activity than their female counterparts (Wright *et al.,* 2001a), with dominants performing more duties than subordinates. Dwarf mongoose subordinate males were reported to perform the most sentinel activity (up to 89% in some cases) in one study (Rasa, 1986), although a subsequent study found dominants to perform more sentinel activity than subordinates, with the difference becoming more apparent as group size increased (Kern *et al*., 2016). Moreover, dwarf mongooses that have recently immigrated into a new group contribute less than residents, likely due to the physical costs of dispersing (Kern and Radford, 2017). As such, previous immigrants contribute the same as resident individuals after five months in their new group (Kern and Radford, 2017). In most reported cases, sentinel behaviour is also influenced by group size: as group size increases, overall coverage increases, whilst individual contributions decrease (Rasa, 1989; Clutton-Brock *et al*., 1999; Ridley and Raihani, 2007). Although well studied, most examples of differential sentinel contributions focus on overall measures such as proportion time as a sentinel, and likelihood of a bout occurring, with less attention given to more specific, or within-bout measures.

1.3.2 Sentinels, satiation and safety

To become a sentinel, an individual must make the decision to forego foraging, therefore sentinel behaviour is intrinsically linked to condition and satiation levels. Individual meerkats who had lost body mass due to babysitting showed reduced sentinel effort the following day, with the suggestion this was due to a reduced nutritional state (Clutton-Brock *et al*., 2002), as seen with recently

immigrated individuals in dwarf mongooses (Kern and Radford, 2017). Mass gain was a predictor of sentinel behaviour in male meerkats (Clutton-Brock *et al.*, 2002), and modelling has shown that it is possible for a coordinated sentinel system to evolve and become stable based only on selfish decisions about an individual's internal state of satiation (Bednekoff, 1997), an idea originally posited by Gaston (1977). Indeed, it is known in multiple species that sentinel contributions are influenced by satiation levels. Florida scrub jays, pied babblers, and Arabian babblers all performed more sentinel activity when given supplementary food (Wright *et al.*, 2001c; Bednekoff and Woolfenden, 2003; Bell *et al.*, 2010). Similarly, meerkats fed 25 g of hard-boiled egg exhibited 30% more sentinel activity than on days when they were not fed (Clutton-Brock *et al.,* 1999). These experimental studies provide clear-cut evidence demonstrating that satiation level can affect the likelihood of sentinel contributions.

One assumption that is often proposed is that the sentinel is safe and therefore less likely to be predated due to its heightened vigilance (Wright *et al.*, 2001a). Indeed, meerkat sentinels are, on average, closer to safety than foragers (Clutton-Brock *et al.*, 1999), but there is no direct link to lower predation rates. Conversely, experimental evidence has shown that pied babbler sentinels are usually further from cover and take longer to reach safety when a predator is identified by an alarm call. In addition, they were the target of over 80% of raptor attacks witnessed (Ridley *et al.*, 2013). Modelling has shown, however, that performing a sentinel bout can still increase an individual's safety whilst acting on purely selfish motives, even if it draws all attempted predation attempts from potential predators (Bednekoff, 2001, 2015). In the model developed it was shown that performing a sentinel bout would increase an individual's safety, because the reduction in undetected attacks outweighs the cost of increased targeting by adopting a prominent position (even up to being targeted in 100% of attacks). This theory is partially supported by the activity of nomadic 'floater' Arabian babblers, who perform sentinel behaviour in the absence of conspecifics although at a lower level than when in a group (Ostreiher and Heifetz, 2017). This demonstrates that personal anti-predatory benefits can be sufficient to warrant performing the behaviour, but in this case they are not enough to explain all the variation seen. These 'floater' individuals also produce alarm calls at the same rate as sentinels within

groups, indicating that such alarm calls could be more important in predator–prey, rather than within-species, communication.

1.3.3 Danger and the Watchman's song

Another modulator of investment in sentinel behaviour is perceived danger; as sentinel behaviour is primarily an anti-predator behaviour, it would be expected that it shows variation in the face of changing threat levels. This is seen in observations of chestnut-crowned babblers (*Pomatostomus ruficeps*): groups performed more sentinel bouts in areas with higher predation pressures (Sorato *et al.*, 2012), resulting in a fivefold increase in probability of a bout between highest and lowest predation pressures. Similarly, meerkats in habitats with fewer predators (ranchland) show ~44% less sentinel coverage than in areas with higher predator density (national park) (Clutton-Brock *et al.*, 1999). At a finer scale, some animals respond to seasonal variation in predation pressure: Florida scrub jays guard more in autumn and winter — seasons with more raptor species present — than spring and summer (McGowan and Woolfenden, 1989). This is not a uniform response, however, as Arabian babblers have not been observed to alter their sentinel contributions during months with highest raptor densities (Wright *et al.*, 2001a). Shorter term responses can be seen both observationally and experimentally. Chestnut-crowned babblers were four times as likely to perform a bout after a predator encounter than in the same time period before the encounter (Sorato *et al.*, 2012). The same qualitative result was found when pied babblers were presented with both heterospecific mobbing playbacks and model snake presentations, although the magnitude of the effect was significantly smaller (1.5 and 2 times increase in probability of becoming a sentinel, respectively) (Ridley *et al.*, 2010).

One within-bout behaviour modulated by perceived danger is the Watchman's song; these surveillance vocalisations act to inform the foraging group of the presence of the sentinel, and are modulated by threat level. Pied babbler sentinels call at faster rates when they perceive the situation to be dangerous (Bell *et al.,* 2009), enabling foraging individuals to optimise their decision-making: during playback of higher-rate surveillance calling, foragers displayed greater personal vigilance than

during playback of lower-rate surveillance calling. Additionally, foragers were more likely to flee following an alarm call if previously played higher-rate surveillance calls (Bell *et al.,* 2009).

1.3.4 Sentinels and their audience

The likelihood that an individual becomes a sentinel is also influenced by its audience and their state. For example, meerkats are more likely to become a sentinel when in the company of pups (Santema and Clutton-Brock, 2013), and chestnut-crowned babbler groups were seven times as likely to have a sentinel present when juveniles or fledglings were with the group (Sorato *et al*., 2012). Furthermore, pied babblers monitor the satiation levels of fellow foragers and make decisions about their sentinel contributions accordingly (Bell *et al*., 2010). Both sentinels (surveillance calls) and foragers (close calls) vocalised at lower rates after receiving supplementary food, and sentinels produced shorter bouts when foragers were more satiated. Moreover, when lower-rate forager calls were played back, longer gaps between sentinel bouts appeared, compared to situations with higher-rate forager playback, which was interpreted as an unwillingness of individuals to become a sentinel when others are also satiated. This suggests individuals are constantly evaluating their surroundings based not only on who is nearby, but how hungry they are, and therefore how likely they are to perform a sentinel bout.

Just as sentinels appear unwilling to perform bouts when others are seemingly well fed, foragers are also less likely to produce bouts if other individuals have performed more sentinel behaviour. When certain Arabian babblers were given supplementary food, thus producing more sentinel activity, non-fed individuals reduced their contribution incompletely, such that the overall coverage increased but the effort of each non-fed individual decreased (Wright *et al*., 2001c).

1.4 Dwarf Mongooses

1.4.1 Life history and general behaviour

The dwarf mongoose is a group-living cooperatively breeding mammal found throughout Eastern and Southern Africa (Rasa, 1977). Inhabiting savannah and plains habitats, the dwarf mongoose is Africa's

smallest carnivore: whilst their diet predominantly consists of arthropods and other invertebrates, they can opportunistically catch snakes, lizards and small mammals (Rasa, 1977). Family groups comprise a dominant pair who are responsible for the majority of the breeding — one genetic study revealed 15% and 24% extra-pair maternity and paternity rates, respectively (Keane *et al.*, 1994) — and non-breeding subordinate helpers who aid in the raising of the young (Rood, 1980).

Dwarf mongooses participate in a range of cooperative behaviours. Individuals maintain social bonds with groupmates by grooming one another (Rasa 1977; Kern and Radford, 2016), subordinate females allolactate young pups, and all adults participate in babysitting and pup feeding during the breeding season (Rasa, 1977; Rood, 1978). Dwarf mongooses also collectively mob potential predators such as snakes and lizards (Kern and Radford, 2016). The individual that discovers the threat emits a specific mobbing call, which acts to recruit other individuals to the area; individuals are more likely to respond to the mobbing calls of group mates with whom they have stronger grooming associations compared to those with which they have a weaker bond (Kern and Radford, 2016).

The dwarf mongoose has many natural predators. The highest threat is from avian taxa: large raptors such as the African hawk-eagle (*Hieraaetus spilogaster*), brown and black-chested snake eagles (*Circaetus cinereus* and *C. pectoralis* respectively) (Kern and Radford, 2014), and smaller hawks such as the pale-chanting goshawk (*Melierax canorus*) and grasshopper buzzard (*Butastur rufipennis*) (Rasa, 1986). In some areas, raptors alone cause mongoose groups an average of 1.5 disturbances per hour (Rasa, 1986). However, there are also many terrestrial predators. The most likely to pose a risk are other mammals: African civet (*Civettictis civetta*), serval (*Leptailurus serval*), caracal (*Caracal caracal*), honey badger (*Mellivora capensis*), black-backed and side-striped jackals (*Canis mesomelas* and *C. adustus* respectively), and white-tailed, banded and slender mongooses (*Ichneumia albicauda*, *Mungos mungo*, *Galerella sanguinea* respectively). Various reptiles, including black mambas (*Dendroaspis polylepis*), Mozambique spitting cobras (*Naja mossambica*), snouted cobras (*Naja haj*e), and puff adders (*Bitis arietans*), also present a threat (Sharpe, *et al.,* 2010).

In response to such diverse predation, a system of functionally referential alarm calls has evolved, with specific calls for aerial and ground predators (Beynon and Rasa, 1989; Collier *et al*., 2017). On spotting an avian predator, individuals produce a pulsed alarm call which results in other group members scanning the sky and seeking cover under rocks and foliage. If a terrestrial predator is detected, then a lower, single-element alarm call is given which causes foraging individuals to seek higher ground and scan the ground and horizon for the threat. Moreover, dwarf mongooses produce terrestrial alarm calls in response to secondary predator cues, such as heterospecific alarm calls or predator faeces (Collier *et al*., 2017).

Dwarf mongooses eavesdrop on the alarm calls of heterospecifics, foraging as part of mixed species groups predominantly with southern yellow-billed hornbills (*Tockus leucomelas*), red-billed hornbills (*Tockus erythrorhynchus*) (Sharpe *et al.*, 2013) and fork-tailed drongos (Herremans and Herremans-Tonnoeyr, 1997). Much like flocks of wading birds (Owens and Goss-Custard, 1976), dwarf mongooses will respond to the alarm calls of multiple species with whom they share predators (Magrath *et al*., 2015). Previous work has shown that dwarf mongooses played alarm calls of tree squirrels (*Paraxerus cepapi*) respond as strongly as when played conspecific alarm calls (Morris-Drake *et al.*, 2017).

1.4.2 Sentinel behaviour

The sentinel system of the dwarf mongoose is typical of similar cooperative species. Individuals adopt a raised position and produce both alarm calls and surveillance calls (Kern and Radford 2013; Collier *et al.,* 2017). Similar to other species, there is a positive relationship between group size and percentage cover (Rasa, 1989). Furthermore, dominant individuals increase their contributions as group size increases, with the opposite trend appearing for subordinate individuals (Kern *et al.,* 2016). In this study, dominant individuals also used higher posts for their bouts, and provided surveillance calls which were perceived to be more reliable: foraging subordinates exhibited less vigilance when played the surveillance calls of a dominant individual than those from a subordinate group member (Kern *et al.*, 2016).

Consistent with the fact they live under high predation pressure, dwarf mongooses modulate their sentinel contributions with information about danger. Playback of a conspecific alarm call increased the likelihood that a sentinel would be present in the following 10 min by 26% compared to playback of a control call (Kern and Radford, 2014). In a subsequent study, individuals were found to become sentinels sooner following conspecific alarm call playbacks, and guarded for longer when these alarms calls were played during their sentinel bout (Kern and Radford, 2014). Contrary to the change in surveillance calling rate seen in pied babblers (Ridley, 2009), dwarf mongoose sentinels reduce their surveillance calling rate when exposed to alarm calls during a bout (Kern and Radford, 2013).

Dwarf mongooses also reward individuals that perform more sentinel behaviour with extra grooming, exhibiting contingent cooperation (Kern and Radford, 2018). Although in this particular study, extra grooming was received equally from all classes of individual, this could be a result of the methodology. Sentinel surveillance calls were broadcast to the whole group, and therefore would likely have benefitted all foragers equally. Should an individual become a sentinel preferentially closer to certain individuals, it could follow that those would be the individuals who would provide the majority of the contingent grooming. Through this mechanism, selective investment in sentinel behaviour based on proximity to certain individuals could lead to increased social bond strength.

1.5 Study Site and Population

The study was conducted at the Dwarf Mongoose Research Project (DMRP), based at Sorabi Rock Lodge, Limpopo Province, South Africa (24° 11'S, 30° 46'E). The reserve is situated in Africa's savannah biome, a flat landscape of wooded foliage and kopjes (granite outcrops). The main vegetation comprises trees — corkwood (*Commiphora mollis*), marula (*Sclerocarva birrea*), knobthorn (*Acacia nigrescens*) — and smaller foliage, such as bush willow (*Combretum spp.*), thorn bushes (*Acacia spp.*) and raisin bushes (*Grewia spp.*) (Sharpe *et al.*, 2010). The climate is characterised by cold winters (May to August) and hot summers (September to April) with most precipitation occurring during October to April (Kern and Radford, 2013).

The study population was made up of six habituated groups of dwarf mongooses (mean ± SE group size = 13.8 ± 1.9, range = 9–22). Individuals were identifiable by a series of blonde hair dye marks (Wella, Weybridge, UK) applied to their fur with a paint brush on an elongated stick, or recognisable features such as scars or morphological irregularities. The DMRP has been running continuously since 2011 and so life history data are known for most individuals. Dominance status was inferred from dominance interactions such as foraging displacements, with the dominant pair identified by scent marking and greeting behaviours (Rasa, 1977). Adult individuals (those over one year of age, and who had therefore survived at least one winter) were classed as either dominant (one pair per group) or subordinate (the remaining individuals), with pups categorised as individuals under one year of age.

1.6 Study Aims

This study was designed to investigate the effects of context-dependency on cooperative behaviour. Using sentinel behaviour as a model behaviour, and dwarf mongooses as a model system, three different contexts were investigated: how variation in satiation and danger levels (and their interaction), and the presence of a conspecific audience, affect sentinel contributions. By using novel measures of sentinel attentiveness, the study aimed to measure sentinel contributions more precisely than previous work and thus to help elucidate the factors which affect cooperative decision-making processes. By further understanding these context-dependent contributions to cooperative behaviour, the study also aimed to increase our understanding of the evolution and maintenance of cooperation.

Chapter 2 — Context-Dependent Contributions to a Cooperative Behaviour: Satiation, Danger and Audience Effects on Sentinel Behaviour

2.1 Abstract

Cooperative behaviours are found throughout nature, with contributions highly variable between and within individuals. Contributions are affected by fixed and long-term variables such as gender, age and dominance status, as well as shorter term factors such as satiation, danger and audience, which form an individual's personal context. Sentinel behaviour (where an individual adopts a raised position to scan for danger and warn groupmates of the presence of predators) is a cooperative act which conveys benefits to group members, as well as providing benefits to the sentinels themselves. Here I manipulate satiation state, perceived danger level and the conspecific audience to investigate the relevance of context-dependency in sentinel contributions. In addition to standard measures of sentinel behaviour (time spent as a sentinel, number of bouts, bout duration), I use novel measures of within-bout investment to investigate sentinel contributions through proxies of attentiveness. Experiments show that dwarf mongoose (*Helogale parvula*) foragers were more likely to become a sentinel when satiated and when under increased danger level, whereas the presence of a neighbouring forager (audience) decreased contributions. Satiation level had the largest impact, with supplementary feeding causing investment in more and longer bouts, whilst a decrease in average head scanning rate provided evidence for an interaction between the effect of satiation and danger levels. These results demonstrate that sentinel contributions are strongly context-dependent, with effects seen in both overall and within-bout characteristics.

2.2 Introduction

Cooperation, "a behaviour which provides a benefit to another individual" (West *et al*., 2007), is widespread in nature. There are many examples of cooperative behaviour throughout the animal kingdom, including with respect to hunting (Boesch, 1994; Creel and Creel, 1995; Bshary *et al*., 2006), the defence of communal territories (Taborsky, 1984; Radford, 2003; Seddon and Tobias, 2003), and in combating predation (Owings and Coss, 1977; Seyfarth *et al*., 1980a; Novaro *et al*., 2009). Cooperation is particularly prevalent in cooperatively breeding species, where non-breeder 'helper' individuals forego their own reproduction to aid the dominant group members in rearing their offspring (Emlen, 1991; Jennions and Macdonald, 1994; Clutton-Brock, 2002; Koenig and

Dickinson, 2004). In such species, individuals cooperate in many activities including food-finding and capture, territory defence, offspring provisioning and protection, and anti-predator behaviour (including coordinated vigilance) (Rood, 1980; Taborsky, 1984; Dawson and Mannan, 1991; Graw and Manser, 2007; Bell *et al.*, 2009; Radford and Kern, 2016). Contributions to these behaviours are variable, with individuals modulating their investment with respect to long- and short-term factors.

Some variation in cooperative contributions is due to differences in the costs and benefits of investing for individuals of different gender, age and dominance status. Members of cooperatively breeding groups differ in various characteristics, fixed either permanently (e.g. gender) or over relatively long periods (e.g. age and dominance status), that can affect cooperative contributions. For instance, male meerkats (*Suricata suricatta*) contribute more than females in the mobbing of venomous snakes (Graw and Manser, 2007), whilst female helper acorn woodpeckers (*Melanerpes formicivorus*) provide more food for young than their male counterparts (Koenig *et al.*, 1983). Regarding age, Damaraland mole rats (*Fukomys damarensis*) increase their contributions to cooperative behaviours such as nest digging as they get older (Zöttl *et al.*, 2016). With respect to dominance status, dominant cichlids (*Neolamprologus pulcher*) contribute more to territorial defence than subordinate individuals (Desjardins *et al.*, 2008). However, not all variation in cooperation can be explained by these relatively fixed characteristics.

Cooperative contributions can show a strong context-dependency, with investments varying in response to shorter term internal, environmental and social factors. For example, individual satiation level (also referred to as state) has been shown to influence brood provisioning, with increased satiation leading to higher rates among both breeding white-winged choughs (*Corcorax melanorhamphos*) (Boland *et al.*, 1997a) and non-breeding Arabian babblers (*Turdoides squamiceps*) (Wright and Dingemanse, 1999). Similarly, satiation level was found to affect rates of 'false feeding' (where an individual feigns feeding of young, but consumes the food itself) in crows (*Corvus corone*), with this deceptive behaviour occurring less frequently when individuals were satiated (Canestrari *et al.*, 2010). Due to the potentially costly nature of anti-predator behaviours, danger

levels are also known to influence cooperative contributions: red-breasted nuthatches (*Sitta canadensis*) preferentially contributed to mobbing behaviour when the threat to themselves was greater (Templeton and Greene, 2007), whilst herring gulls (*Larus argentatus*) increased their alarm calling as danger increased (Shah *et al.*, 2015). There are also audience effects on cooperative contributions: the presence of a conspecific prevented cheating through false feeding in white-winged choughs (Boland *et al.*, 1997b), and led to increases in alarm calling in red-legged partridges (*Alectoris rufa)* (Zaccaroni *et al.*, 2013). However, only a few studies have investigated the effects of such contexts in relation to sentinel contributions, with no studies to my knowledge attempting to investigate potential interactions of the effects of changing context on cooperative investment.

Here, I investigate context-dependent contributions to sentinel behaviour in the dwarf mongoose (*Helogale parvula*). Sentinel behaviour, where an individual adopts a raised or prominent position to look out for danger (Bednekoff, 2015), has evolved in mammals (Rasa, 1986; Clutton-Brock *et al.*, 1999), birds (McGowan and Woolfendon, 1989; Bell *et al.*, 2009) and possibly fish (Fox and Donelson, 2014). Sentinel behaviour is cooperative, with alarm calls given to warn group mates of potential predators, whilst the presence of a sentinel enables foragers to exhibit less vigilance (Hollén *et al.*, 2008; Rauber and Manser, 2017), which in turn leads to a higher food intake (Hollén *et al.*, 2008). This is achieved through a system of surveillance calls (also known as the 'Watchman's song') to announce the sentinel's presence (Hollén *et al.*, 2008; Kern and Radford, 2013); production of these low-amplitude vocalisations is a cooperative act (Hollén *et al.*, 2008). There is some evidence that sentinel contributions can be influenced by context: individuals are more likely to perform sentinel bouts when fed (Wright *et al.*, 2001c; Bednekoff and Woolfenden, 2003), and are less likely to perform sentinel duties if others are in a more favourable state (Bell *et al.*, 2010). Individuals also contribute more to sentinel behaviour, and modulate their surveillance calls accordingly (Bell *et al.*, 2009), when danger levels are increased (Ridley *et al.*, 2010; Sorato *et al.*, 2012). Further change in investment is seen conditional on the audience present, with individuals more likely to invest in sentinel behaviour when with young than in their absence (Sorato *et al.*, 2012; Santema and Clutton-Brock, 2012).

The majority of previous studies on sentinel contributions have focussed on general measures of sentinel coverage (e.g. likelihood a bout occurs, number of bouts, time spent as a sentinel); only a few within-bout measures, such as vocalisations (Bell *et al.*, 2010; Kern and Radford 2013) or sentinel height (Kern and Radford, 2014), have been considered, with no studies into differential attentiveness. It is thus far not known if sentinels are more attentive, and therefore valuable as guards, under certain contexts; it is conceivable that sentinels are more alert when danger level is higher, or when they have more resources to contribute. Sentinels may also differentiate their investment by participating in self-serving behaviours such as grooming or social monitoring. It is also known that animals integrate multiple stimuli into decision making processes, which can often interact (Hebets and Papaj, 2005; Morris-Drake *et al.*, 2016) and therefore could significantly impact on sentinel contributions. However, potential short-term modulators of sentinel contributions have thus far been experimented in isolation (Clutton-Brock *et al.*, 1999; Wright *et al.*, 2001a, c; Sorato *et al.*, 2012), with no attempts to investigate any potential interactions between such short-term contextual contributors.

Cooperatively breeding dwarf mongooses provide an ideal study species in which to investigate the effects of context-dependency on sentinel behaviour. Dwarf mongooses forage in groups for predominantly invertebrate prey (Rasa, 1989) and face large predation pressure from raptors and terrestrial predators such as small felids and snakes (Sharpe *et al.*, 2010; Kern and Radford, 2014). Whilst foraging, individuals spend considerable time with their heads down searching or digging for prey, and therefore face a trade-off between vigilance and food-finding. Perhaps as a consequence, dwarf mongooses have evolved both a sentinel system (Rasa, 1986) and to eavesdrop on the alarm calls of heterospecifics such as fork-tailed drongos (*Dicrurus adsimilis*) and tree squirrels (*Paraxerus cepapi*) (Rasa, 1986; Morris-Drake *et al.*, 2017). Previous work has shown that dwarf mongooses increase their sentinel contributions in response to conspecific alarm calls, with their surveillance calls decreasing in rate (Kern and Radford, 2014). However, there has been no consideration of other context-dependent responses, including the integration of different factors, examination of the influence of heterospecific warnings of danger, or measurement of fine-tuned alterations in sentinel

behaviour during a bout. The latter, as well as controlled field-based experimentation is facilitated because wild dwarf mongooses can be habituated to the close presence of observers (Kern and Radford, 2013).

Specifically, I use supplementary feeding and playback manipulations to investigate how sentinel contributions are affected by satiation and danger levels (and their interaction), and by conspecific audience effects. I monitored the general measures of sentinel activity (i.e. likelihood of becoming a sentinel, time to first bout, number of bouts, bout duration) and more fine-scale within-bout characteristics such as vocalisations, scan rate, and distraction. With respect to satiation level, I predicted that supplementary feeding would result in individuals performing sentinel bouts sooner, more frequently and for longer, and that there would be a greater scanning rate and more vocalisations per bout, if sentinels increase contributions when their state is favourable (Bednekoff, 1997; Clutton-Brock *et al*., 1999; Wright *et al*., 2001c). With respect to danger level, I predicted that a simulated increase in predation risk would result in individuals becoming a sentinel sooner, performing longer bouts, scanning at a higher rate, and being less likely to become distracted or vocalise, due to an increased vigilance associated with the heightened personal risk and subsequent safety consequences (Wright *et al*., 2001a; Ridley *et al*., 2010). With respect to an audience effect, I predicted that the simulated close presence of a conspecific would lead to a greater likelihood that a sentinel bout was performed, an increase in the number of bouts and duration of bouts, as well as lower distraction levels and more vocalisations, if individuals are using sentinel contributions as a sexual signal of prestige (Zahavi, 1990; Zahavi and Zahavi, 1997) or for more immediate grooming rewards (Kern and Radford, 2018).

2.3 Methods

2.3.1 Study site and population

The study was conducted at the Dwarf Mongoose Research Project (DMRP), based on the Sorabi Rock Lodge reserve, Limpopo Province, South Africa (24° 11'S, 30° 46'E). The study site is in Southern Africa's Savannah Biome and experiences a Lowveld climate. The year is distinctly split into two

seasons: the hot rainy season running from September to April, and the cold dry season from May to August (Kern and Radford, 2013). Data were collected between March and July 2018. The study population comprised six wild groups of dwarf mongooses (mean ± SE group size = 13.8 ± 1.9, range = 9–22), habituated to the close presence of human observers (Kern and Radford, 2013, 2014) and individually identifiable by a system of blonde dye-marks added to their fur (Wella, Weybridge, UK). The study animals are habituated and trained to climb on a balance scale using a reward of hard-boiled egg (Kern and Radford, 2013, 2014). The DMRP has been running constantly since 2011, therefore each individual has a known gender, dominance status and life history. Only adult individuals (those which were at least one year old) were used in the study; adults were categorised as either dominants (one pair per group) or subordinates (all other adults) through observations of aggressive behaviour, foraging displacements and scent marking (Kern and Radford, 2013; Kern *et al*. 2016).

At the study site, dwarf mongooses face many natural predators, both aerial and terrestrial. These include: raptors such as African hawk-eagles (*Hieraaetus spilogaster*), brown snake-eagles (*Circaetus cinereus*) and pale-chanting goshawks (*Melierax canorus*) (Rasa, 1986; Kern and Radford, 2014); mammals such as black-backed jackals (*Canis mesomelas*), servals (*Leptailurus serval*), banded mongooses (*Mungus mungo*) and slender mongooses (*Galerella sanguinea*); and reptiles such as black mambas (*Dendroaspis polylepis*), puff adders (*Bitis arietans*), Mozambique spitting cobras (*Naja mossambica*) and rock monitors (*Varanus albigularis*) (Sharpe *et al.,* 2010). In response to the heavy predation pressure, dwarf mongooses exhibit both personal vigilance and cooperative sentinel behaviour, whereby an individual adopts a prominent raised position to scan for danger whilst the other group members forage (Rasa, 1986; Kern and Radford, 2013, 2014). Due to their arthropod-based diet, dwarf mongooses spend a large amount of time digging with their head down, meaning they must trade-off foraging and vigilance as the two behaviours are mutually exclusive (Rasa, 1989). The sentinel system provides protection to foragers; the sentinel provides updates on current danger levels through surveillance calls, and produces alarm calls when a predator is spotted (Kern and Radford, 2013, 2014). Dwarf mongooses also spend much time foraging in groups with other species,

predominantly fork-tailed drongos, and yellow-billed (*Tockus leucomelas*) and red-billed (*Tockus erythrorhynchus*) hornbills (Sharpe *et al.*, 2010). As these species all share a host of predator species, especially raptors, dwarf mongooses respond to the alarm calls of all three species, as well as other informers such as grey go-away birds (*Corythaixoides concolor*) and tree squirrels (Sharpe *et al.*, 2010; Morris-Drake *et al.,* 2017).

2.3.2 Experimental overview

Two experiments were run over the course of the field season. Experiment 1 ran from March to May 2018, and Experiment 2 from May to July 2018.

Experiment 1 tested the effects of satiation level and danger level (and any interaction between the two) on sentinel contributions. This experiment adopted a 2x2 design, with each focal individual receiving a feeding treatment followed by a playback treatment. Feeding treatments were: Feed — the provision of 1/4 hard-boiled egg; and Non-Feed — the provision of a few egg crumbs (as a control). The focal individual would then receive one of two playback treatments: Danger — the playback of tree squirrel alarm calls, or Non-Danger — the playback of tree squirrel close calls (as a control). Fifteen individuals were targeted to receive all four treatment combinations (Feed x Danger, Feed x Non-Danger, Non-Feed x Danger, Non-Feed x Non-Danger) but, for logistical reasons, four of the 15 individuals only received two combinations instead.

Experiment 2 tested the effects of a conspecific audience on sentinel contributions. This experiment had a paired design, with each focal individual presented with two playback treatments: close calls (low-amplitude vocalisations given whilst foraging; Rasa, 1986) from the opposite gender dominant within their group (chosen as the standardised experimental 'audience'); and ambient sound (as a control). Twenty individuals received both playback treatments.

2.3.3 Playback track preparation

Playback tracks were prepared from original recordings of dwarf mongoose close calls, tree squirrel close and alarm calls, and ambient sound. All recordings were made using a Sennheiser MKE600 shotgun microphone (Sennheiser, Wedemark, Germany) paired with a Marantz PMD661 MkIII solid state recorder (Marantz, Kanagawa, Japan). The microphone was mounted in a Rycote lyre shock mount (Rycote, Stroud, UK) to isolate handling noise, with all recordings taken in still conditions to maximise audio clarity. Recordings of dwarf mongoose close calls were made from up to 3 m away, whereas the tree squirrel close and alarm calls were made from a greater distance (up to 10 m) due to their lack of habituation to human observers. Ambient-sound recordings were made from the centre of each group's territory. Sound pressure level (SPL) readings were taken using a HandyMAN TEK1345 sound meter (Metrel UK Ltd., Normanton, UK) in order to determine the natural amplitude for use during playbacks. Recordings were isolated using the noise reduction functions in Adobe Audition CC (Adobe Systems, San Jose, USA). Playback tracks were compiled in Reaper (Cockos Inc., New York, USA), and exported at a sample rate of 44.1 kHz.

For Experiment 1, 230 s tracks were created for both playback treatments. Each track contained eight calls: tree squirrel alarm calls in the Danger treatment, and tree squirrel close calls in the Non-Danger treatment. These eight calls were spaced in two 25 s blocks each containing four calls, with 3 min of silence between the blocks (Figure 2.1). In total, 19 unique alarm calls and 17 unique close calls were used, with four unique calls used per track. The design was blocked so that within any group, no individuals would be played the same calls and thus habituation effects were minimised. Each individual received the same playback track for both Danger trials and for both Non-Danger trials; different tracks were used for different individuals.

For Experiment 2, 10 min tracks were created for both treatments. In the 'audience' treatment, close calls were played at a naturally determined rate (5 calls/min; J. Kern, personal communication) overlaid on an ambient-sound recording. In the control treatment, only the ambient-sound track was

played, with each pair of tracks played to an individual created using the same ambient-sound recording.

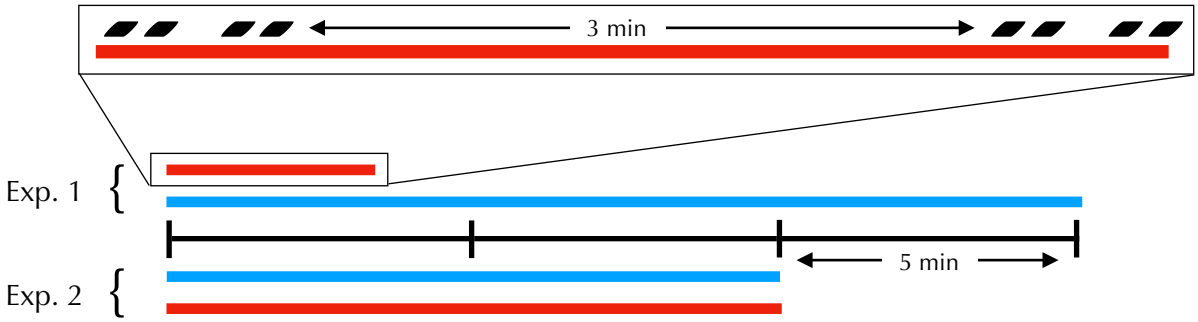


Figure 2.1 Timeline of the observation period (blue) and the playback tracks (red) for Experiment 1 (above timeline) and Experiment 2 (below timeline). For Experiment 1, specific placement of each call is shown by a black rhombus within the expanded view. For Experiment 2, calls were evenly spaced at a rate of 5/min for the duration of the playback starting at 6 s into the track.

2.3.4 Experimental trials

2.3.4.1 General procedure

For both experiments, trials were conducted during the morning (0700–1200) and afternoon (1300–1800) field sessions, when the group were foraging away from a sleeping burrow. Trials on the same individual were run within a 2 h window on separate days, to maximise the possibility that both environmental conditions and individual behavioural/satiation states were as similar as possible. All trials on any one individual occurred over a maximum period of 14 days. Multiple trials were run on separate individuals within a group on a given day, with at least 30 min between the end of one trial and the start of the next in order to minimise potential carry-over effects.

A trial was commenced only if a set of environmental and behavioural criteria were met. The majority of individuals in the group had to be foraging, with the group in their own territory, and with no or only light wind. There had to have been no alarm calls from either conspecifics or tree squirrels for 10 min, no latrine or mobbing events for 30 min, and no inter-group interactions for 3 h (adapted from

Kern and Radford, 2014). If any of the above disruptions occurred during a trial, it was terminated. If a trial had run for at least 5 min of the observation period, the trial was considered complete. If the disturbance happened before 5 min of observation had occurred, the trial was considered incomplete and subsequently repeated (Experiment 1: N = 15; Experiment 2: N = 10). For Experiment 2, trials were also not commenced or were terminated if the individual whose close calls were being played back moved within 3 m of the focal individual for a period longer than 10 s, to maximise the likelihood playback was the major stimulus.

2.3.4.2 Experiment 1 specifics

Once the relevant general experimental trial conditions were met (see above), the focal individual received its feeding treatment (Feed or Non-Feed). In both treatments, the relevant food (1/4 hard-boiled egg or a few crumbs, respectively) was delivered from a plastic pot by hand to the focal individual. The Non-Feed treatment controlled for potential confounding effects of the individual feeding from the pot, interacting at a close distance with the experimenter, or any feedback associated with the ingestion of egg; the latter is especially relevant as the entire study population is habituation trained using egg for the purposes of close observation, dye-marking and weighing.

After completion of the feeding treatment, a 30 s 'break' period (to allow the focal individual to resume normal activity; duration determined by pre-experiment pilot tests) was followed by the playback treatment (Danger or Non-Danger). Experimental tracks (tree squirrel alarms or close calls, respectively) were played using an iPhone 7 (Apple Inc, Cupertino, USA) connected to a Bose Soundlink Micro loudspeaker (Bose Corporation, Framingham, USA) via Bluetooth. The loudspeaker was anchored at a height of 110 cm on the belt of the experimenter, and oriented towards the focal individual at all times. Both tree squirrel close and alarm calls were played back at 45 dB at 1.5 m. This alarm call amplitude was lower than that used in Morris-Drake *et al.* (2017) to minimise the likelihood of an immediate flee response.

Whenever possible, each individual received all four possible experimental conditions (Feed x Danger, Feed x Non-Danger, Non-Feed x Danger, Non-Feed x Non-Danger), and these were assigned so that each individual received a unique trial order. Within each group, individuals were counterbalanced in a Latin square, so that no individual received the same treatment in the same sequence position as another group member. The intention was to minimise a trial order effect, especially as dwarf mongooses have previously shown a tendency to habituate rapidly to both playbacks and predator presentations (A. Radford and J. Kern, personal communication).

2.3.4.3 Experiment 2 specifics

Once the relevant general experimental trial conditions were met (see above), the focal individual received one of the two playback treatments: close calls of the opposite gender dominant or ambient sound. The order of treatment presentation was counterbalanced between individuals. Experimental tracks were played back using the same equipment as in Experiment 1, but the loudspeaker was anchored to the ankle of the experimenter at a height of 10 cm — the natural height at which close calls from adjacent conspecifics occur. Ambient-sound tracks (40 dB at 10 m) and close-call tracks (45 dB at 1.5 m) were played back at their natural amplitudes (Morris-Drake *et al.*, 2017).

2.3.5 Data collection

In both experiments, the sentinel behaviour of the focal individual was monitored during the trial. Trials were filmed from 2–5 m with a Canon 70D DSLR camera with a Canon 50 mm f1.8 lens (both Canon Inc, Tokyo, Japan). Audio recording was embedded in the video track via an attached RODE VideoMic Pro shotgun microphone (RODE Microphones, Sydney, Australia). The experimenter dictated information that might not have been clear on the video/audio recordings: confirmation of any vocalisations and commentary on any scanning activity or potential distraction. In Experiment 1, filming occurred from the start of the playback for 15 min. In Experiment 2, focal individuals were filmed for 10 min, also from the beginning of the playback.

Videos were watched back using VLC Media Player (VideoLAN, Paris, France) to record detailed information on sentinel behaviour. A sentinel was classed as an individual that adopted a position with its feet at least 10 cm above the ground and remained vigilant for >10 s (as in Kern and Radford 2013, 2018). Data categories extracted for each sentinel bout were: time from start of trial (s); duration of bout (s); number of surveillance calls; number of head scans (one scan was classified as a movement between two distinct head positions); and time distracted (number of seconds performing behaviours which likely reduce vigilance: scratching, self-grooming, grooming of others, sleeping). For bout duration and number of head scans, a mean value was taken from all bouts within each trial. Furthermore, a scan rate per min was calculated ((scan number / duration of bout) * 60) to control for bout duration. After a provisional analysis of the data, both distraction and vocalisation data were converted into binary measures (Yes/No) as the datasets were not large enough to assess more fine-tune differences accurately. Videos were unable to be scored blind due to the requirement of audio for dictation purposes, which clearly picks up the type of playback being presented.

2.3.6 Statistical methods

Data were analysed using R statistics build version 3.4.4 (R Core Team). Mixed models were used due to the repeated sampling of individuals and groups created by the matched design. Linear Mixed Models (LMMs) were run using the 'lme' function from the nlme package, whilst Generalised Linear Mixed Models (GLMMs) were run using the 'glmer' function from the lme4 package. Normally distributed data were tested with LMMs, whilst non-normal data were transformed where possible using square/cube root or log transformations. Where data were not transformable to fit the assumptions of parametric testing, model fitting was used to find a suitable error distribution with which to run a GLMM. In the case of all binary data, a binomial distribution was fitted with a logit-link function. For all models, Individual ID was nested within Group ID as a random term.

To begin analysis, a maximal model was created by fitting all relevant terms. Stepwise backwards elimination was then used to remove non-significant terms (Crawley, 2005) until the minimal model remained: the model at which further removal of terms caused a significant loss in explanatory power.

This was determined by running a Chi Squared test on the model with and the model without the term in question; a significant difference between these two models indicated a loss of explanatory power. Significant terms were subsequently removed from the minimal model one at a time, with the comparison between the resulting model and the minimal model generating the displayed X^2 and p values. Similarly, non-significant terms were tested by individually re-adding them to the minimal model. The effect size and standard error (SE), alongside the intercept values and the variance ± SE for random terms were all derived from the minimal model.

2.4 Results

2.4.1 Experiment 1

2.4.1.1 Likelihood a bout is performed

The likelihood that an individual performed a sentinel bout was significantly affected by both satiation level (feeding treatment) and danger level (playback treatment) (Table 2.1; Figure 2.2). Individuals were more likely to become a sentinel following a Feed treatment compared to a Non-Feed treatment, and also following a Danger compared to a Non-Danger treatment. However, there was no significant interaction between the factors (Table 2.1).

Table 2.1. Factors affecting whether an individual performed a sentinel bout (Generalized Linear Mixed Model).

Fixed Effect	X^2	d.f.	p	Effect ± SE
Feeding	**11.518**	**1**	**<0.001**	**1.590 ± 0.805**
Playback	**4.538**	**1**	**0.0332**	**2.604 ± 0.930**
Trial Duration	0.425	1	0.515	
Trial Order	0.207	1	0.977	
Feeding:Playback	0	1	0.999	
Intercept				-0.587 ± 0.591
Group ID				0.134 ± 0.365
Individual ID				0.00 ± 0.00

Significant fixed effects in bold, random effects italicised. A binomial error distribution was fitted to the data using the link-logit function (N_{Groups} = 5, $N_{Individuals}$ = 15, N_{Trials} = 52).

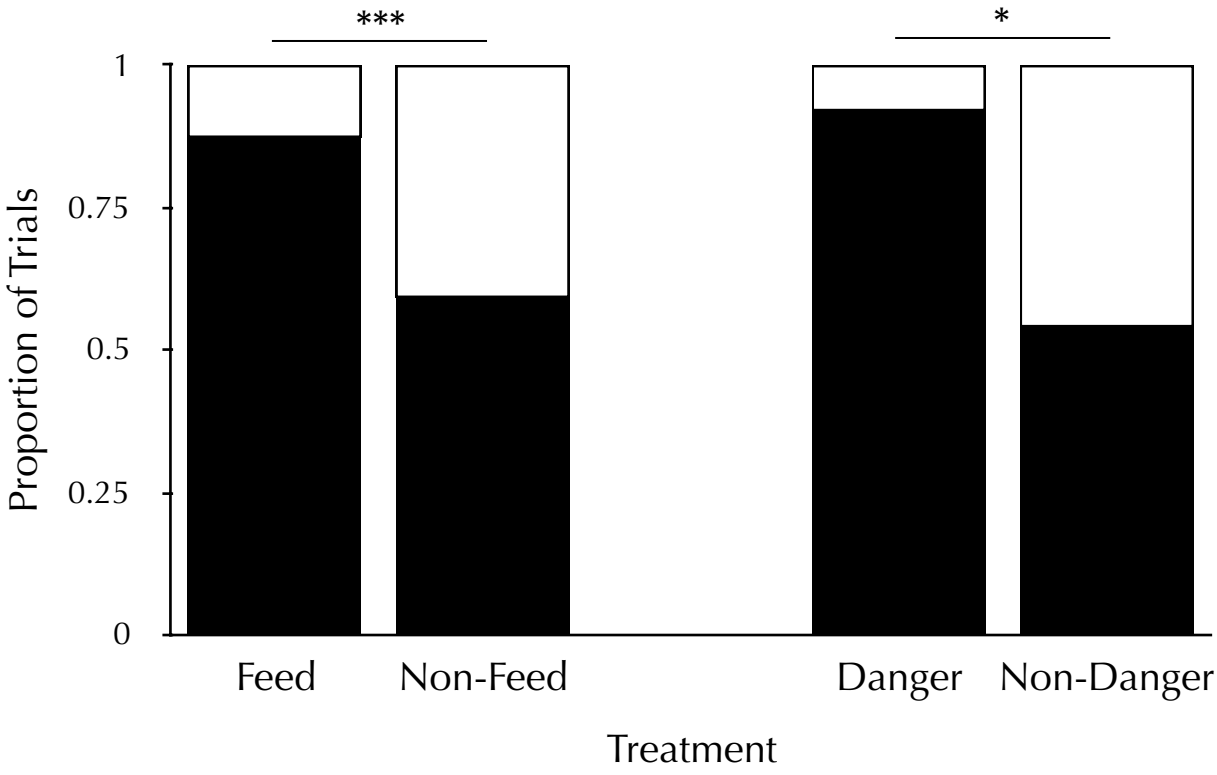


Figure 2.2. The effect of feeding and playback treatments on the likelihood that an individual performed a sentinel bout. Black bars indicate trials where a sentinel bout was performed, with white bars representing trials where no sentinel bout was performed. Significance codes: *** = < 0.001; * = < 0.05. $N_{Groups} = 5$, $N_{Individuals} = 15$, $N_{Trials} = 52$.

2.4.1.2 Overall bout characteristics

Time until the first sentinel bout and number of sentinel bouts performed were both significantly affected by satiation level (Table 2.2). The provisioning of 1/4 egg resulted in a shorter time until a bout was performed (Figure 2.3a) and a greater number of bouts (Figure 2.3b) than in control trials. There was no significant effect of danger level on time until first bout (Table 2.2b), but there was a non-significant trend for playback treatment to affect the number of bouts performed, with a greater number of bouts seen following alarm-call playback compared to control playback (Figure 2.3b). There was no significant interaction between the feeding and playback treatments on either the time until the first sentinel bout or the number of bouts performed (Table 2.2).

Table 2.2. Factors affecting a) time until the first sentinel bout was performed (Linear Mixed Model), and b) number of sentinel bouts performed (Generalised Linear Mixed Model).

Fixed Effect	X^2	d.f.	p	Effect ± SE
a) Time to first bout				
Trial Order	**7.066**	**1**	**0.0079**	**2.492 ± 0.932**
Feeding	**4.298**	**1**	**0.0382**	**-4.276 ± 2.089**
Feeding:Playback	0.819	2	0.664	
Playback	0.173	1	0.677	
Intercept				7.461 ± 2.856
Group ID				<0.001 ± <0.001
Individual ID				<0.001 ± <0.001
b) Number of bouts				
Feeding	**6.622**	**1**	**0.0101**	**0.584 ± 0.230**
Playback	3.422	1	0.0643	0.422 ± 0.228
Feeding:Playback	2.754	2	0.0970	
Trial Order	6.001	1	0.112	
Trial Duration	0.294	1	0.588	
Intercept				0.0867 ± 0.222
Group ID				0.0430 ± 0.207
Individual ID				0.0427 ± 0.206

Significant fixed effects in bold, random effects italicised. Variance ± SE given for random terms. Data for a) were square-root transformed ($N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 38), whilst for b), a Poisson distribution was fitted using the log-link function ($N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 79).

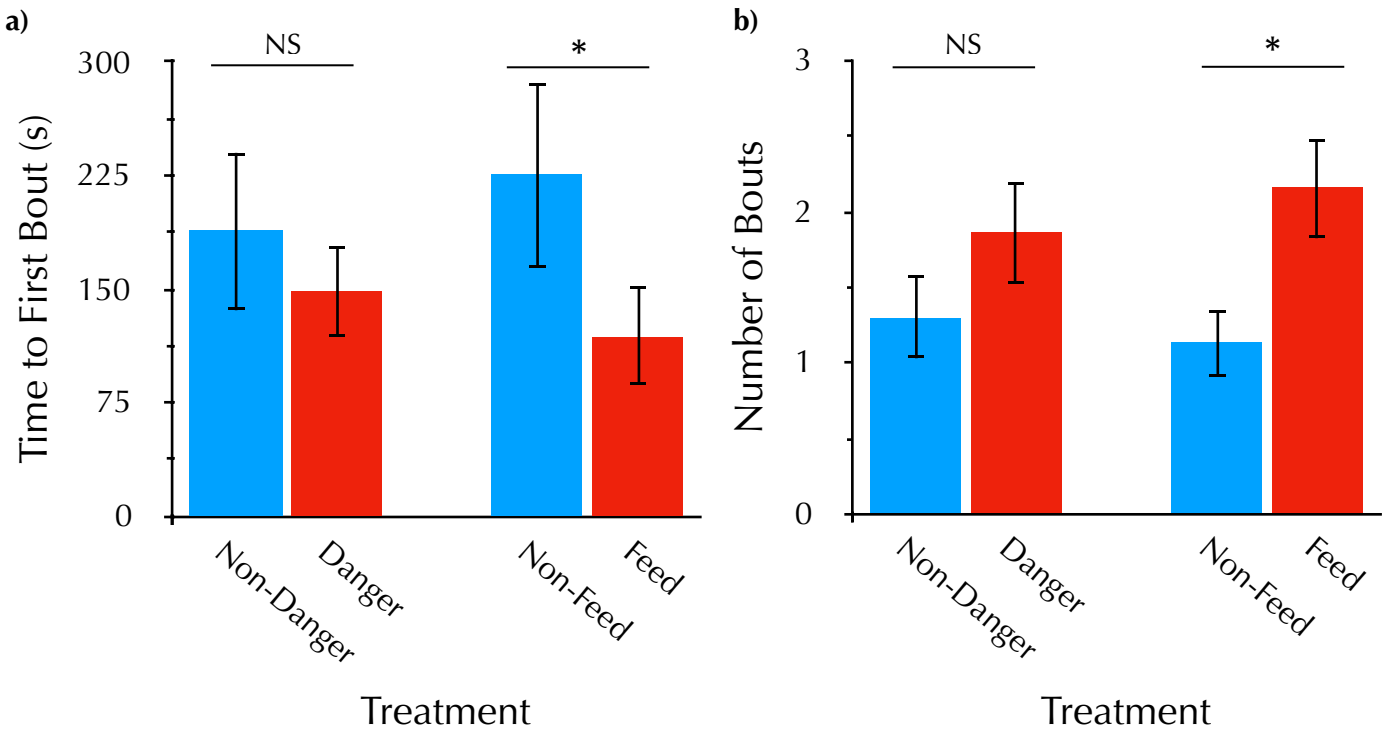


Figure 2.3. Effect of feeding and playback treatments on a) time to first sentinel bout and b) number of bouts performed. Bars represent group means, error bars are SE. Significance codes: * = < 0.05; NS = non-significant. a: $N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 38; b: $N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 79.

2.4.1.3 Within-bout characteristics

Mean bout duration was significantly affected by satiation level (Table 2.3a): bouts were longer in the Feed treatment than the Non-Feed treatment (Figure 2.4a). Trial order also had a significant effect on mean bout duration: as trial order progressed, the mean bout duration decreased (Table 2.3a). Neither danger level nor its interaction with satiation level had a significant effect on mean bout duration (Table 2.3a).

Mean scan rate during a bout was significantly negatively affected by the duration of the sentinel bout (Table 2.3b). There was also a significant effect of the interaction between the feeding and playback treatments: scan rate was higher in the Danger than the Non-Danger treatment, but this effect was smaller when the individual was fed rather than unfed (Table 2.3b; Figure 2.4b).

Table 2.3. Factors affecting a) mean sentinel bout duration and b) mean scan rate of the sentinel during their bout (Linear Mixed Models).

Effect	X^2	d.f.	p	Effect ± SE
a) Mean bout duration				
Trial Order	**4.251**	**1**	**0.039**	**-0.194 ± 0.009**
Feeding	**3.942**	**1**	**0.042**	**0.399 ± 0.197**
Playback	5.187	1	0.158	
Feeding:Playback	5.315	1	0.257	
Intercept				3.550 ± 0.282
Group ID				0.069 ± 0.262
Individual ID				<0.001 ± <0.001
b) Mean scan rate				
Bout Duration	**8.125**	**1**	**0.004**	**-0.111 ± 0.040**
Feeding:Playback	**3.993**	**1**	**0.046**	**-8.616 ± 4.506**
Playback	3.550	1	0.060	
Feeding	1.082	1	0.298	
Trial Order	0	1	0.995	
Intercept				27.706 ± 3.168
Group ID				<0.001 ± <0.001
Individual ID				<0.001 ± <0.001

Significant fixed effects in bold, random effects italicised. Variance ± SE given for random terms. For a), data were log transformed. ($N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 79).

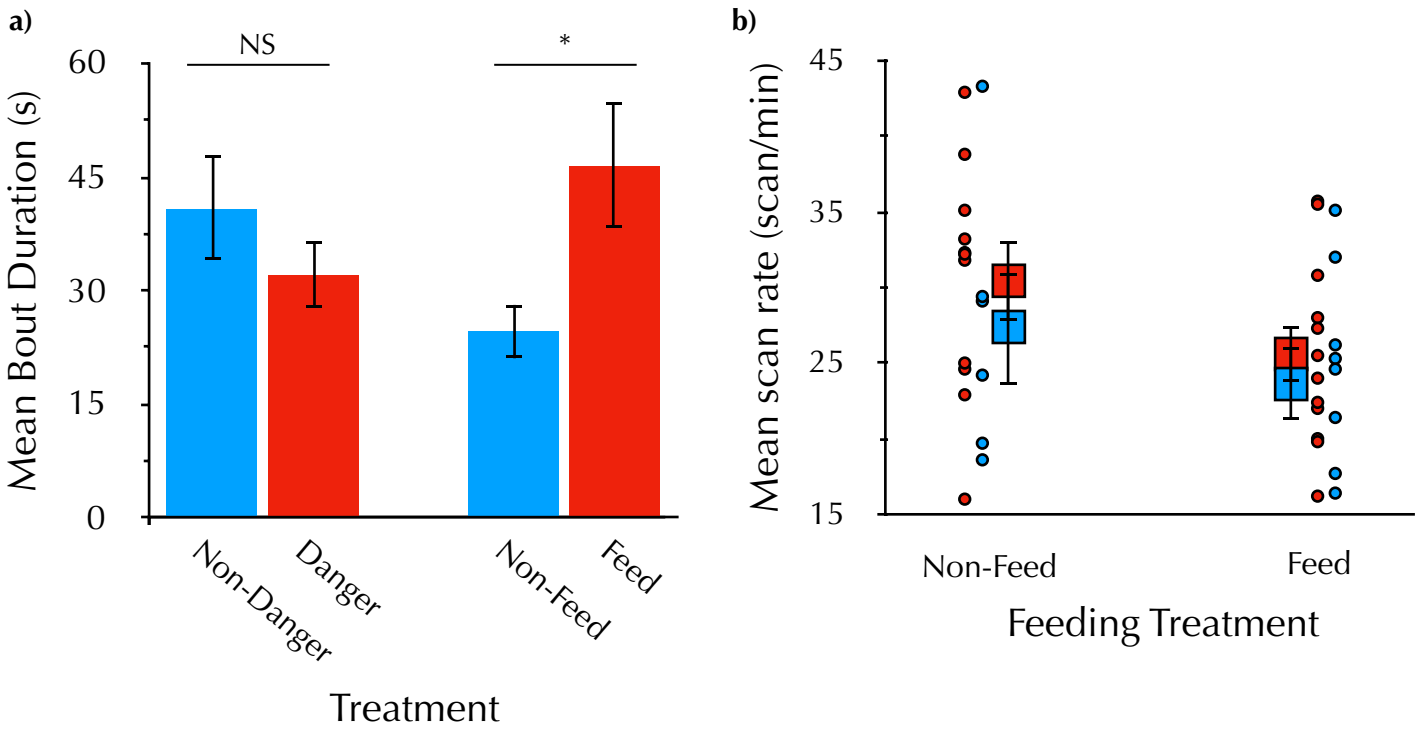


Figure 2.4. Effect of feeding and playback treatments on a) mean bout duration and b) mean scan rate. Group means represented by a) bars and b) boxes, error bars are SE. For b), red points represent Danger playback treatment, with blue representing the Non-Danger control, with all points displayed. Significance codes: * = < 0.05; NS = non-significant. $N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 79.

The likelihood that an individual vocalised during a sentinel bout was not significantly affected by feeding treatment, playback treatment or their interaction (Table 2.4a). The likelihood that an individual became distracted during a sentinel bout was significantly positively affected by the duration of the bout (Table 2.4b). There was a non-significant trend for the interaction between feeding and playback treatments to affect the likelihood of distraction (Table 2.4b): distraction levels were higher in the Danger compared to the Non-Danger treatment, with this effect more prominent when the individual had been fed compared to unfed.

Table 2.4. Factors affecting a) whether a sentinel vocalised during a bout and b) whether a sentinel became distracted during a bout (Generalised Linear Mixed Models).

Effect	X^2	d.f.	p	Effect ± SE
a) Vocalisation				
Feeding	0.054	1	0.817	
Playback	0.118	1	0.731	
Feeding:Playback	0.168	1	0.983	
Trial Order	1.269	1	0.260	
Bout Duration	1.198	1	0.274	
Intercept				-0.770 ± 0.242
Group ID				<0.001 ± <0.001
Individual ID				<0.001 ± <0.001
b) Distraction				
Bout Duration	**18.447**	**1**	**<0.001**	**0.039 ± 0.012**
Playback	3.741	1	0.053	1.173 ± 0.640
Feeding:Playback	7.493	1	0.058	2.321 ± 1.488
Feeding	0.691	1	0.406	
Trial Order	0.174	1	0.677	
Intercept				-2.213 ± 0.458
Group ID				<0.001 ± <0.001
Individual ID				<0.001 ± <0.001

Significant fixed effects in bold, random effects italicised. Models fitted with binomial error using a logit-link function. Variance ± SE given for random terms ($N_{Individuals}$ = 15, N_{Groups} = 5, N_{Bouts} = 79).

2.4.2 Experiment 2

2.4.2.1 Likelihood a bout is performed

The likelihood that a sentinel bout was performed was significantly affected by playback treatment (Table 2.5; Figure 2.5). Individuals performed bouts in 11 of the 20 control trials, but in only four of the 20 trials when there was playback of the close calls of the simulated audience.

Table 2.5. Factors affecting whether an individual performed a sentinel bout (Generalised Linear Mixed Model).

Fixed Effect	X^2	d.f.	p	Effect ± SE
Treatment	**6.186**	**1**	**0.013**	**-1.942 ± 0.974**
Trial Order	2.026	1	0.155	
Intercept				0.589 ± 0.745
Group ID				0.170 ± 0.412
Individual ID				0.909 ± 0.954

Significant terms highlighted bold, random effects italicised. Model fitted with binomial error using a logit-link function. Variance ± SE given for random terms (N_{Groups} = 5, $N_{Individuals}$ = 20, N_{Trials} = 40).

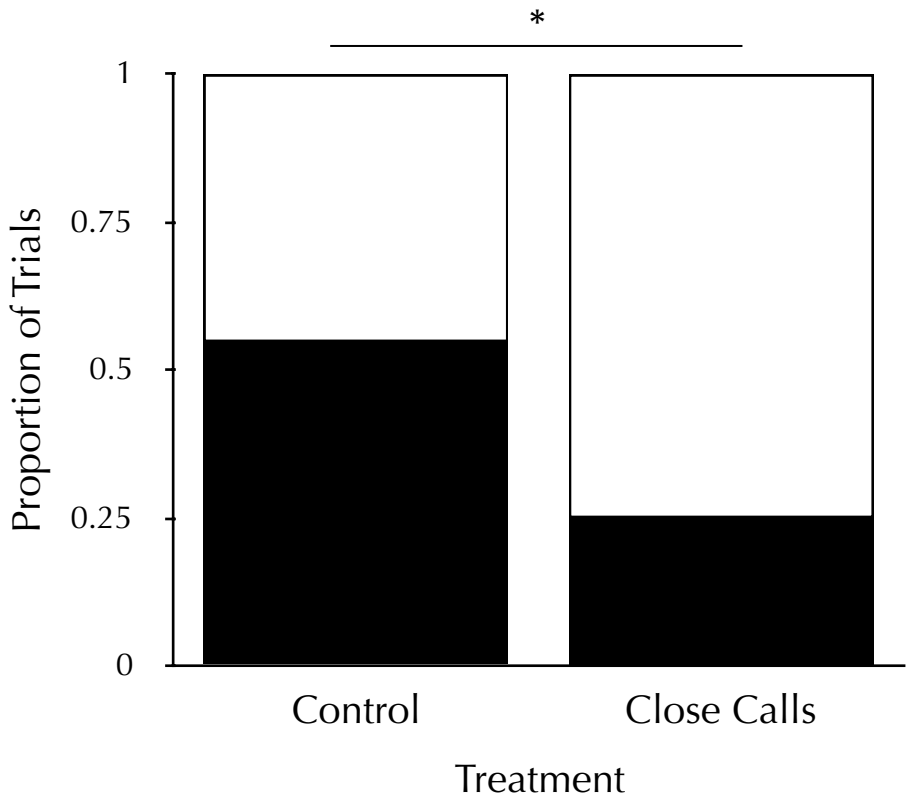


Figure 2.5. Effect of conspecific audience presence simulated by close call playback on likelihood that an individual became a sentinel. Black bars represent trials with sentinel bouts, with white bars showing trials where the focal individual did not perform a bout. Significance code: * = <0.05. N_{Groups} = 5, $N_{Individuals}$ = 20, N_{Trials} = 40.

2.4.2.2 Other response variables

Due to the low number of sentinel bouts performed (sentinel bouts occurred in 15/40 trials, N_{Bouts} = 28), and the majority occurring during the control trials (11/15 trials, 19/28 total bouts), there was insufficient statistical power to examine effects of the playback treatment on other response variables.

2.5 Discussion

Dwarf mongooses altered their sentinel contributions in response to changes in satiation level, danger level and the presence of a conspecific audience. This work therefore presents further evidence for the context-dependent nature of sentinel behaviour, with new insight for both its effects on within-bout characteristics and how multiple factors can interact to influence cooperative behaviour.

2.5.1 Experiment 1

Satiation level had a significant effect on overall sentinel behaviour, with supplementary food resulting in increased investment. Additional food resulted in a greater likelihood that an individual became a sentinel, as well as reducing the time until the first sentinel bout and increasing total number of bouts performed compared to control conditions. These results are qualitatively similar to previous empirical studies on the effects of satiation on sentinel behaviour in other species (Clutton-Brock *et al*., 1999; Wright *et al*, 2001c; Bell *et al*., 2010), and match the predictions of the theoretical model produced by Bednekoff (1997). This satiation effect could be indicative of at least some 'selfish' element to the sentinel system, although data on the relative safety of dwarf mongoose sentinels and foragers would be required to consider this in detail. However, it is unlikely that this investment is entirely selfish as dwarf mongoose sentinels receive direct benefits from groupmates; individuals increase their grooming of those that have invested more in sentinel behaviour (Kern and Radford, 2018). These experimental results therefore indicate a satiation effect on cooperative contributions.

Overall sentinel behaviour was also significantly affected by danger level, though to a lesser extent than the influence of satiation level. There was a trend for a higher danger level to induce more sentinel bouts, although no effect was seen on time until first bout. Such responses provide further

evidence for the theory that overt vigilance should increase with perceived risk (Lima and Bednekoff, 1999), and are qualitatively similar to those of Kern and Radford (2014), as well as in other similar species (Ridley *et al*., 2010; Sorato *et al*., 2012). That individuals are more likely to become a sentinel under increased danger also agrees with the predictions of theories that sentinels are safer than foragers (Bednekoff, 1977; Wright *et al*., 2001a), and as such should perform bouts when danger level is higher. However, a similar increase would also be predicted if benefits of sentinel behaviour are accrued through kin or reciprocal means, as a sentinel conveys greater benefit to foragers when danger is high than when low. Further experimentation is required to disentangle whether an increased likelihood of becoming a sentinel is driven by an increased perception of danger primarily to the individual (personal selfish means — by-product mutualistic development), or danger to the group (cooperative/altruistic means — reciprocal/kin selected development). It is likely that both elements are relevant, and provide benefits in differing proportions based on the individual circumstances.

The significant effects of danger level in Experiment 1 provide further evidence that dwarf mongooses alter their behaviour in response to information from heterospecifics, as the relevant playbacks were of tree squirrel alarm calls. The alarm calls were played back at a lower amplitude than previously investigated (Morris-Drake *et al*., 2017) in order to increase perceived danger levels without eliciting alarm responses consistent with immediate predator presence. That the study individuals responded appropriately to this stimulus demonstrates that dwarf mongooses not only eavesdrop on heterospecific alarm calls in relation to immediate predation events, but integrate them into the decision-making process governing sentinel behaviour. Concurrent with information use in similar species (Bell *et al*., 2009; Ridley *et al*., 2010), dwarf mongooses appear to use heterospecific information to gather information about current threat level and alter their cooperative contributions accordingly.

With regards to within-bout characteristics, evidence for an effect of the interaction between satiation and danger levels was seen. Mean scanning rate was higher under danger playback, but this increase

was significantly less obvious when individuals were fed rather than when they were unfed. This reduction in apparent attentiveness is seemingly counterintuitive, as it could be predicted that a) sentinel attentiveness is unrelated to satiation level, or b) increased resources from a higher satiation level can be invested as increased attentiveness. It is possible that higher scanning rate should not be viewed as a measure of higher attentiveness; individuals who are more vigilant may fixate gaze on potential threats more readily, thus lowering their scanning rate and apparent attentiveness. The trend for distraction to be affected by the interaction between satiation and danger levels is more difficult to rationalise. Distraction levels were higher in individuals experiencing increased danger levels, with feeding increasing this likelihood further. Increased levels of scratching and grooming — self-directed behaviour that has been proven to be indicative of increased stress levels in other species (Schino *et al*., 1996) — could conceivably result from the increased threat of predation. Conducting such behaviours whilst acting as a sentinel would seem potentially maladaptive, as an individual would appear to be less vigilant when scratching and grooming than actively scanning. However, the relative vigilance cost of these distractions are not yet quantifiable; it is possible that such behaviours only negligibly reduce sentinel attentiveness, similar to incomplete reductions seen in foragers (Lima and Bednekoff, 1999). Furthermore, in this study, alarm calls were played back at a lower level than in previous studies, so as not to cause immediate flee and alarm responses. The cost of momentary lapses in attention would likely be less costly under such danger levels than if a threat was imminent.

2.5.2 Experiment 2

Contrary to the predicted effect, sentinel investment was reduced in the presence of a nearby conspecific audience. This may suggest that individuals are not conducting sentinel bouts when in the close presence of conspecifics, reducing the likelihood that prestige effects are the driving force behind sentinel contributions (Zahavi, 1990; Zahavi and Zahavi, 1997). This parallels results from chestnut-crowned babblers (*Pomatostomus ruficeps*), where prestige effects have been shown not to be important in provisioning of young, which is a similarly costly cooperative act (Nomano *et al*., 2013). The reduction in sentinel effort could be explained, however, by an individual-level manifestation of the group-size effect, where an increased group size results in lower individual

contributions (Rasa, 1989; Clutton-Brock *et al.*, 1999; Ridley and Raihani, 2007). It is unlikely that individuals are able accurately to monitor complete sentinel coverage, forager spread and potential group splits in the dense habitat found at the project site. Thus, it is possible that sentinel investment could also be influenced by smaller scale feedback loops, with individuals assessing their immediate environment (i.e. number and identity of conspecifics), and performing more sentinel behaviour when surrounded by fewer nearby conspecifics.

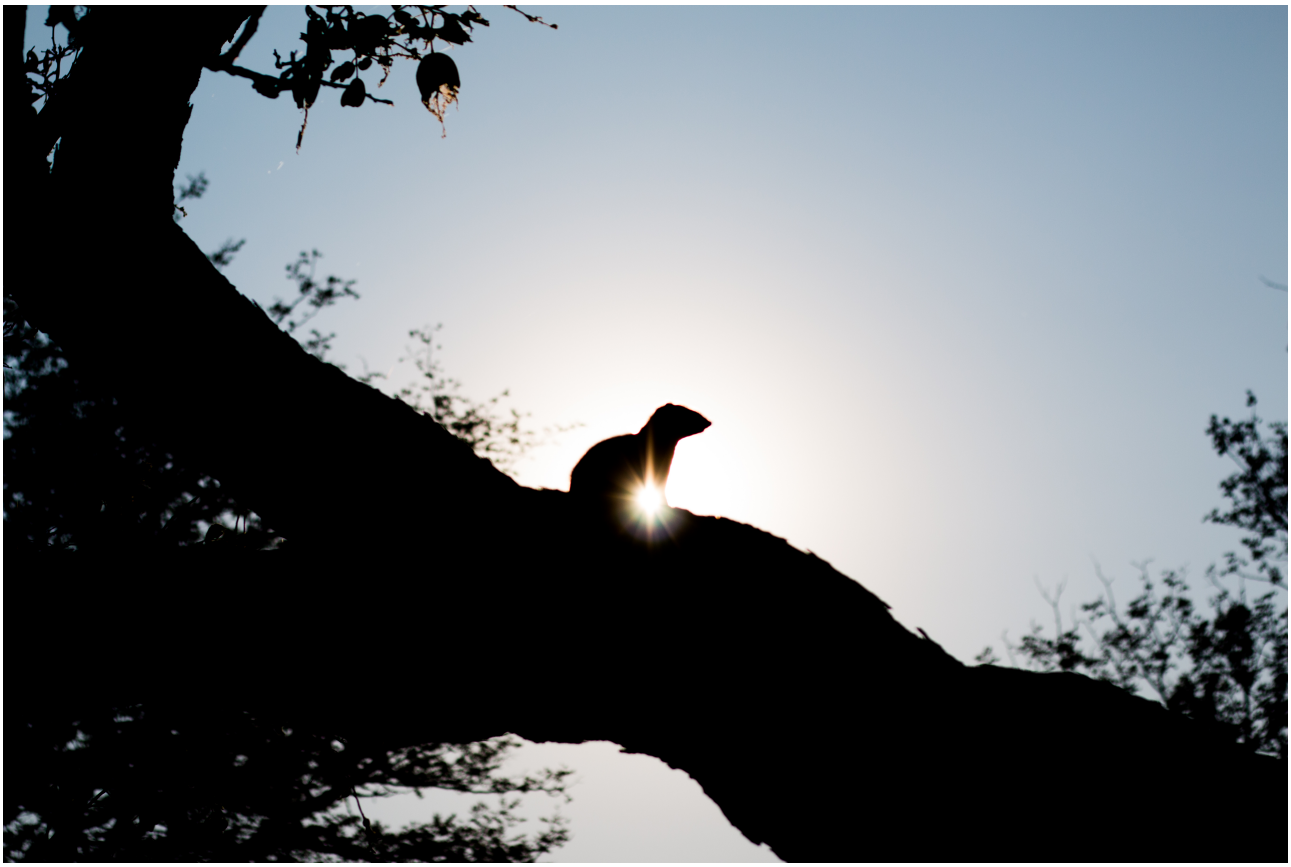
An alternative explanation for the decrease in sentinel contributions when the presence of a nearby conspecific was simulated relates to the contributions of others. Previous work has shown that pied babblers are less likely to become a sentinel when a conspecific is in a good state, as conveyed in the close-call rate (Bell *et al.*, 2010). It is possible that dwarf mongoose close calls not only convey identity (Rubow *et al.*, 2017) but also state information, which would therefore cause a reduction in the sentinel contributions of the focal individual. A third possible explanation is based on the effect that an audience has on the perception of personal danger. An accompanied individual is expected to be less vigilant than an isolated individual (Radford and Ridley, 2007); should this decrease be due to a decreased personal danger level, then it follows that individuals exposed to the experimental audience would be less likely to perform a bout as sentinel behaviour is more likely when the situation is dangerous (as discussed in 2.5.1). It is unlikely that just one of these theories is sufficient to explain the decrease in sentinel contributions shown here, and they are certainly not mutually exclusive mechanisms. It is probable that individuals are integrating some, or all, of the above information and making an informed decision based on their own current perception of their own contribution, the contributions of others and their own personal risk.

2.5.3 Conclusions

My study corroborates previous findings with regards to the effects of satiation and danger levels on sentinel contributions, with increases in both satiation and perceived danger causing individuals to increase their investment in sentinel behaviour — with satiation level showing the larger effect. I also provide the first evidence that these two factors interact to influence sentinel decisions, with scanning

rate and potentially distraction likelihood affected by the integration of these two factors. By using novel measures of within-bout attentiveness, I achieved fine-tune assessment of sentinel contributions; this increased scrutiny of sentinel behaviour has demonstrated that context does alter the characteristics of bouts, with further work required to confirm how these changes influence predator detection and subsequent benefits to foragers. I also demonstrate how an audience can reduce sentinel contributions, although the mechanisms for this remain unclear. Overall, sentinel contributions exhibit strong context-dependency, with both overall and within-bout characteristics affected.

Chapter 3 - General Discussion



3.1 Study Findings

This study demonstrated that the decisions governing overall sentinel characteristics (likelihood of becoming a sentinel, number of bouts, time to first bout) and the associated within-bout characteristics (mean bout duration, head scanning and distraction) are dependent on individual context in dwarf mongooses (*Helogale parvula*). The satiation level of an individual had the largest effect on sentinel contributions, with elevated satiation levels resulting in an increased likelihood of performing a bout, an increase in mean bout time and number of bouts, and a decrease in latency to first bout. Qualitatively similar changes in contributions were caused by elevated danger levels, although only the likelihood of performing a bout was a significant response factor. Satiation and danger levels interacted to reduce the scan rate within bouts, compared to when they acted alone, as well as potentially increasing distraction rates. The opposite effect was seen in the presence of a conspecific audience, with the likelihood of becoming a sentinel significantly lower when a nearby audience was simulated.

These results largely agree with previous work on context-dependent contributions to sentinel behaviour. Satiation level produced the predicted changes in contributions to both overall and within-bout characteristics, as seen in similar studies (Clutton-Brock *et al*., 1999; Wright *et al*., 2001c; Bell *et al*., 2010). Danger level also produced changes in contributions, qualitatively matching my predictions as well as previous studies (Ridley *et al*., 2010; Sorato *et al*., 2012; Kern and Radford, 2014), but with a smaller effect than satiation level; danger level did not affect certain bout characteristics, and produced non-significant trends in others. These results match the predictions of models on safe and selfish sentinel activity (Bednekoff, 1997; Wright *et al*., 2001a), which would suggest that sentinel behaviour is the result of a by-product mutualism where individuals perform the behaviour to satisfy their own personal goals. It is known, however, that dwarf mongoose sentinels actively inform foragers of their presence (Kern and Radford, 2013) whilst gaining reciprocal contingent benefits from group members (Kern and Radford, 2018), so this mutualism is not sufficient to explain either all variations seen in contributions, nor the presence of such vocalisations and reciprocal benefits.

Novel measures of within-bout sentinel activity provided a window into how sentinel attentiveness can be modulated by both satiation level and danger level; head scanning rate and distraction likelihood both changed opposite to predictions made, suggesting sentinels are less attentive when fed under higher danger. This seemingly maladaptive reduction in scanning rate could well be due to misclassification of attentiveness; individuals may be fixating gaze on potential predators more readily, resulting in a lower scanning rate. The increased distraction likelihood could be the result of self-directed behaviour (Schino *et al.*, 1996), and not as costly in detecting predators as it may seem (Lima and Bednekoff, 1999). Regardless of the mechanistic basis, these measures of attentiveness also provide evidence that satiation and danger levels can interact to inform decision-making, as in both scanning rate and distraction likelihood they affected contributions non-independently.

The effect of a nearby conspecific audience was opposite to that predicted, suggesting prestige effects (Zahavi, 1990; Zahavi and Zahavi, 1997) may not be driving variation in sentinel contributions in this species. Such reduction in sentinel contributions could be explained through either group-size effects (Rasa, 1989; Clutton-Brock *et al.*, 1999; Ridley and Raihani, 2007) manifesting at a local level, relative measures of personal danger level based on conspecific presence (Radford and Ridley, 2007), or assessment of the state of other individuals (Bell *et al.*, 2010; Rubow *et al.*, 2017). It is probable that individual foragers are updating their current context with information about personal factors as well as other group-member contributions, and subsequently integrating all of these factors to make decisions about their own investments.

3.2 Study Limitations

The habituation of focal individuals to the alarm call playback, as evidenced by significant effects of trial order on multiple response variables, limited the scope of the study to investigate the effects of danger level, and subsequent interactions with satiation level. This is highlighted by the multiple non-significant trends drawn from the dataset, all of which correspond to either danger level or danger level:satiation level interactions. Identical tracks were used for both danger playbacks in order not to

confound the result with unknown grading of danger level encoded in the alarm calls used, but this led to multiple exposure to the same calls. It is conceivable that on the first hearing of the alarm call individuals learnt it to be unreliable as no predator was present, thus subsequently responding less. Habituation was considered when creating playback tracks (see 2.3.3), but due to the time and group visitation constraints, multiple trials were run concurrently within groups. Although I made my best effort to not commence playback in the direct presence of another focal individual, it is possible that other individuals' playback tracks were heard, and subsequent general habitation occurred. "Reliability reinforcement" of the stimulus could be used in future in order to minimise such habituation effects (Potvin *et al*., 2018).

The provisioning of egg required for the feeding treatments in Experiment 1 greatly limited sample size and explanatory power, as well as potentially introducing a personality bias to the study sample. Although habituated to close observation, and habituation trained with hard-boiled egg, many individuals were not comfortable within the immediate presence (<0.5 m) of the experimenter, a distance required to ensure targeted supplementary feeding. Although the control condition — feeding a few egg crumbs from the handheld pot — controlled for any extra vigilance caused by close approach to the experimenter, a subset of individuals would only approach when the larger amount of egg in the Feed treatment was offered, further reducing the sample size. This confound left a reduced subset of the population for experimentation, which had a larger impact on certain response measures especially as individuals sometimes did not perform a bout during the response period (no bouts in 14/52 trials). Although this did not reduce the sample size for measures such as likelihood of a bout, or number of bouts, all within-bout characteristics were impacted, and thus their explanatory power lowered. It could also be considered that the only individuals experimented upon shared personality traits associated with easy habituation (boldness, lower neophobia etc.). Whilst the matched design of the experiment will have controlled for individual variations, this 'personality sorting' must still be kept in mind.

Due to the wide spread of individuals in dwarf mongoose foraging groups and the density of the habitat at the study site, exacerbated by late summer rains, measures of group behaviour alongside experimental manipulations were impossible to record. Whereas similar studies on individual contributions to sentinel behaviour have contrasted the investment of the individual against that of the group (Wright *et al.*, 2001c), the study was unable to produce such contrasts. Should this or similar studies be repeated, it is recommended that the dry season be chosen as to enable the accurate monitoring of the contributions of the entire foraging group.

3.3 Further study

Sentinel scanning rate, significantly affected by bout duration, needs to be better understood in ultimate terms; what drives changes in scanning rate, and how these subsequent changes affect sentinel attentiveness. The decrease in scanning rate as bouts lengthen could be due to an initial assessment when beginning a bout (higher scanning rate in the first few seconds was anecdotally seen), which then settles to a baseline rate once threat level has been determined and surroundings assessed. A study into how scanning behaviour changes as a bout progresses, including within-bout treatments — i.e. playback during a bout — would help gain clarity on both innate characteristics of vigilance, and how investment is altered relative to changing threat. Furthermore, quantifying the effect of scanning rate on predator detection would enable more informed discussion around changes in its rate.

One aspect of sentinel behaviour that is often overlooked, and one which could contribute greatly to cost mitigation, is the potential for acquiring social information. Group-living species integrate the monitoring of others into their vigilance decisions (Favreau *et al.*, 2010), and therefore it would be likely that individuals performing sentinel bouts could do much the same. Such social monitoring has been discussed in a limited capacity with regards to sentinel behaviour; male meerkats (*Suricata suricatta*) may exhibit increased sentinel contributions due to the opportunity to assess dispersal and mating opportunities (Clutton-Brock *et al.*, 2002). This seems to underestimate the scope of this field, however, as the sentinel's raised position offers it a far greater overview of the group than when

foraging. Information about specific social and sexual partners could be gained, whilst more detailed assessments of foraging efficacy, and in some cases, opportunities to displace could be gathered. During this experimental season, a pilot study was run where sentinels were presented with close-call playback from a foraging individual in either a stationary or moving condition to represent a forager in a good and bad foraging patch, respectively. It was hypothesised that sentinels would conclude their bouts sooner when their closest forager was in a high quality food patch, and subsequently join or displace them. However, the disturbance caused to the sentinel, especially in the moving condition, was too great to gain accurate results in this species, but such opportunities should be explored in similar species.

Another further avenue of study should investigate why individuals appear to contribute less to sentinel behaviour when presented with an experimental audience. Presenting a foraging individual with multiple different audiences — differing dominance classes, genders and ages — would help to uncover what is driving this decision-making process. If an assessment of danger is occurring, then differential contributions will appear with age and dominance as dominant individuals provide more reliable information (Kern *et al*., 2016), whereas if any preferential signalling were occurring, it would follow that a difference between genders would be apparent; strongest social bonds are always across genders (J Kern, personal communication) and therefore would be preferentially acquired where possible. If, however, individuals are merely making assessments based on the contributions of others, it would be unlikely to see a distinct difference in contributions based on the class or gender of the audience.

When calculating indirect benefits to a sentinel, it is vital that individual genetic relatedness is known. Although pedigree analysis allows rough lineages to be created, parentage must be assumed, which does not account for extra-pair parentage seen in dwarf mongooses (Rood, 1980; Keane *et al.*, 1994). Furthermore, there are no estimates of baseline relatedness for dwarf mongoose populations, therefore the relative importance of relatedness between individuals may be over-estimated. This is particularly relevant to the contributions of immigrant individuals. To gain relatedness estimates for

the individuals in the study population, I instigated a programme of DNA relatedness analysis: the organisation of all the required permits, the lining up of suitable collaborators for the laboratory-based extraction and microsatellite analysis of faecal samples (as a means of non-invasive sampling from the population), and initial collection of faecal samples (326 samples collected from 96 individuals). Whilst there was not sufficient time within my Masters for this to be completed, this planned DNA analysis will enable accurate relatedness assessments to be built into models of cooperative contributions in this species in the future.

To make further claims about the relative costs and benefits that drive the variation in sentinel contributions, it is important to have accurate estimates for the parameters involved. As such, measures of safety of a sentinel, such as those calculated for meerkats and pied babblers (Clutton-Brock *et* al., 1999; Ridley *et al*., 2010), are required for dwarf mongooses. It is also important to integrate measures of benefits to receivers of such a behaviour, and how in turn these benefits will convey benefit back to the sentinel. Whilst evidence exists that sentinel contributions produce contingent benefits (Kern and Radford, 2018), it should be further explored how benefits to both sentinels and foragers accrue.

3.4 Conclusions

Individual contributions to cooperative behaviours are modulated by personal context. In this study, I have shown that satiation level, danger level, and the presence of a conspecific audience all alter the sentinel contributions of the dwarf mongoose. Furthermore, individuals modulate their within-bout characteristics relative to their current context, although explanations for these require further investigation. These results add to the body of work suggesting sentinel contributions are highly plastic, and based largely on personal context, as well as helping inform theories of the evolution and maintenance of such behaviours. Future work should aim to more strictly quantify the relative costs of performing such behaviours — including assessing more fine tune measures of the behaviour — as well as the benefits accrued.

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